THESE

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Etude du relâcher de loups (*Canis lupus lupus*) en Russie : méthodes d'élevage, modélisation d'habitat, dispersion et survie

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A Casimir.

C’est à toi qui « annonce la paix » que je dédie ce labeur,
Dont nous aurons vécu ensemble les dernières heures.
Sache que ta venue toute proche me comble de bonheur !

Résumé :

Etude du relâcher de loups (*Canis lupus lupus*) en Russie : méthodes d'élevage, modélisation d'habitat, dispersion et survie

Les réintroductions et translocations d'animaux dans la nature sont effectuées depuis longtemps par l'homme, souvent pour des raisons cynégétiques ou parfois par accident. Avec l'extinction d'espèces, ces méthodes, avec pour but ultime le renforcement des populations, sont devenues un sujet attrayant en biologie de la conservation. Elles ont été utilisées avec succès chez différentes espèces de mammifères et d'oiseaux. Cependant, en ce qui concerne les grands carnivores, potentiellement dangereux pour l'homme et le bétail, peu d'études se sont intéressées à la faisabilité de réintroduction de prédateurs élevés en captivité. Afin de tester l'efficacité de réintroduction du loup gris, j'ai étudié les 64 individus élevés et relâchés à la Station Biologique « Chisty Les » (Toropestky raion, Tverskaya oblast, Fédération de Russie) depuis 1993. L'étude du comportement des loups lors de l'élevage en captivité a permis de dresser des profils comportementaux des individus dont le relâché a été couronné de succès. Le suivi par satellite de loups relâchés n'a donné des résultats qu'à court-terme, mais suffisants pour y voir une tendance à l'adaptation en milieu sauvage. La détermination de leur régime alimentaire par l'analyse d'excréments a montré que les loups se nourrissaient essentiellement de proies sauvages, avec une grande diversité, des insectes aux ongulés, ainsi que de nombreux végétaux. Les résultats de cette thèse démontrent donc la faisabilité de réintroduction de loups élevés en captivité : les individus relâchés présentent des comportements en accord avec leur statut social, ils sont capables de se nourrir, ils se déplacent à distance de l'homme et dispersent vers de nouveaux territoires. Parallèlement, j'ai étudié deux points clés entourant le processus de réintroduction : la définition de l'habitat du loup afin de déterminer les sites de relâché potentiels ; et la performance de colliers pour le suivi satellitaire à une fine échelle des individus relâchés.

Mots-clés : *Canis lupus*, réintroduction, comportement, régime alimentaire, GPS, déplacements, habitat.

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Abstract:

Experimental release of wolves (*Canis lupus lupus*) in Russia: raising methods, habitat suitability, dispersion and survival.

For a long time, human beings have made animal reintroductions and translocations into the wild, often for game reasons, sometimes by accident. With the species' extinction, these methods, with the ultimate goal of populations' reinforcement, became an attracting subject in conservation biology. They were successfully used with various mammal and bird species. However, concerning the large carnivores, potentially dangerous for human and livestock, few studies inquired about the feasibility of reintroduction of captive-raised predators. So as to test the effectiveness of grey wolf reintroduction, I studied 64 individuals raised and released at the Biological Station "Chisty Les" (Toropestky raion, Tverskaya oblast, Russian Federation) since 1993. The study of behaviour of wolves during the raising in captivity allowed setting up behavioural profiles of successful individuals. The satellite monitoring of released wolves only gave short-term results, but sufficient to see a trend of adaptation to the wild. Diet assessed by excrements analysis showed that wolves mainly feed on wild prey, with a great diversity, from insects to ungulates, as well as much vegetation. The results of this thesis thus proved the feasibility of captive-raised wolves' reintroduction: released individuals display behaviours in accordance to their social status, they are able to find food, and they keep a distance to humans and disperse to new territories. At the same time, I studied two key points of the reintroduction process: the definition of wolf habitat so as to determine potential release sites; and the collars performance for satellite monitoring of released individuals.

Key words: *Canis lupus*, reintroduction, behaviour, diet, GPS, movements, habitat.

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Абстракт:

Экспериментальный выпуск волков (*Canis lupus lupus*) в России: методы разведения, оценка среды обитания, рассеивания и сохранения.

В течение долгого времени, люди реинтродуцировали и переселяли животных в дикую природу, часто для охоты или иногда случайно. С исчезновением видов, эти методы, с конечной целью повешения численности, стали привлекательной темой в биологии сохранения. Они успешно использовались с различными видами млекопитающих и птиц. Однако, относительно крупных хищных млекопитающих, потенциально опасных для человека и домашних животных, немного исследований выло проведено по возможности реинтродукции хищников выращенных в неволе. Чтобы проверить эффективность реинтродукции серого волка, я изучила 64 особи выращенные и выпущенные на Биологической Станции «Чистый Лес» (Торопецкий район, Тверская область, Российская Федерация) с 1993 г.. Изучение поведения волков в период содержания их в неволе позволило выявить поведенческие особенности успешно выпущенных особей. Спутниковое слежение за выпущенными волками давали только краткосрочные результаты, но достаточные, чтобы видеть тенденцию адаптации к дикой природе. Определение их режима питания путем анализа экскрементов показало, что волки исключительно питались дикими животными, с большим разнообразием, от насекомых до крупных копытных, а так же с большим количеством растительности. Результаты этой диссертации таким образом доказали возможность реинтродукции волков выращенных в неволе: выпущены особи показывают поведение в соответствии со своим социальным статусом, они способны питаться, они держутся на расстоянии от человека и расселяются на новые территории. Одновременно, я изучила два ключевых момента процесса реинтродукции: определение среды обитания волка, для определения потенциальных мест выпуска; и качество работы спутниковых ошейников для слежения за выпущенными особями.

Ключевые слова: *Canis lupus*, реинтродукция, поведение, режим питания, GPS, перемещения, среда обитания.

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Publications & communications

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Sommaire

Chapter 1. Introduction

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Глава 1. Введение

1.1. Historique et définitions

L'aire de répartition historique du loup gris (*Canis lupus*) s'étendait à tout l'hémisphère nord, avec des limites sud atteignant l'Arabie et l'Inde sur le continent eurasiatique, et le Mexique sur le continent américain (Lohmus 2002). La population actuelle mondiale est estimée à 300.000 individus, ce qui est bien moindre que la population historique (Vilà et *al.* 1999). Suite à une persécution acharnée, le nombre de loups était à son plus bas niveau dans la deuxième moitié du 20ème siècle, l'animal ne vivant plus que dans des zones reculées et sauvages. En Eurasie, les loups avaient quasiment disparu du continent, en-dehors des Apennins en Italie, des Monts Cantabriques en Espagne, des Carpates en Europe de l'Est, des régions septentrionales de l'ex-URSS, des steppes et montagnes d'Asie et des déserts du Moyen-Orient. En Amérique du Nord, les loups ont survécu essentiellement au Canada et en Alaska, et dans l'état sauvage du Minnesota aux Etats-Unis. Grâce à la protection du loup à partir des années 1970, son fort taux de reproduction et son adaptabilité, les populations ont ré-augmenté et recouvré leur habitat. Les loups de l'ex-Union Soviétique colonisent la Finlande, et quelques individus atteignent la population scandinave. Depuis l'Italie du nord, les loups ont reconquis la France et la Suisse ; et les loups polonais s'installent progressivement en Allemagne de l'est. Aux Etats-Unis, la population du Minnesota s'est développée dans les états voisins du Wisconsin, du Michigan et du Dakota, tandis que les loups canadiens ont atteint le Montana, l'Idaho et l'Etat de Washington (Mech 1995). Malgré ce retour progressif du loup et son déclassement en « moins concerné » par l'Union Internationale pour la Conservation de la Nature (IUCN 2011), les risques pour sa conservation existent et incluent la persécution humaine, la chasse, la destruction d'habitat, l'hybridation, les risques génétiques des petites populations isolées, et les maladies. La protection du loup est ainsi inscrite dans la législation de nombreux pays (Table 1.1).

Table 1.1: Le loup dans la législation internationale (source : Landry 2001).

Liste Rouge de l'Union Internationale pour la Conservation de la Nature (IUCN 2011):	Le loup est classé comme espèce à Préoccupation mineure (LC : "*Least concerned*").
Manifesto on Wolf Conservation (1973):	Il comprend une déclaration des principes pour la conservation du loup et donne des lignes directrices pour la conservation du loup. Rédigé en 1973 par le *Wolf Specialist Group* de l'IUCN/SSC, il est régulièrement révisé pour tenir compte de l'évolution du statut du loup (dernière révision le 23.02.2000).
Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 1973):	Le loup y est classé dans l'annexe II (espèce potentiellement menacée), exceptées les populations du Bhoutan, de l'Inde, du Pakistan et du Népal, classées dans l'annexe I (espèces menacées d'extinction).
Convention de Berne (Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe, 1979) :	Le loup y est classé dans l'annexe II (espèce strictement protégée). Plusieurs pays ont obtenu une derogation quant à la protection du loup (Bulgarie, Espagne, Finlande, Turquie, République tchèque, Slovaquie, Pologne, Lettonie et Lithuanie) où il est classé dans l'annexe III (espèce protégée qui peut être soumise à une chasse contrôlée).
Directive des Habitats (membres de l'Union Européenne, 1992):	Le loup y a le statut « d'espèce d'intérêt communautaire prioritaire », devant être protégée. L'article 16 permet toutefois de déroger à ce régime de protection pour prévenir des dommages.

Dans les zones où une recolonisation naturelle du loup a peu de chance de se produire, les options sont la réintroduction ou la translocation. L'UICN définit la réintroduction comme « l'essai d'implanter une espèce dans une zone qu'elle occupait autrefois, mais d'où elle a été éliminée ou d'où elle a disparu ». La translocation est « un déplacement délibéré et provoqué par l'homme, d'individus sauvages vers une population existante de la même espèce » (UICN 1998). Alors que la translocation induit nécessairement le relâcher d'individus capturés dans la nature, la réintroduction peut faire appel à des individus nés en captivité ou capturés en milieu naturel. Toujours selon l'UICN (1998), le principal but de ces méthodes est « d'établir dans la nature une espèce viable en liberté, suite à sa disparition du milieu naturel à l'échelle locale ou mondiale » et les objectifs peuvent être divers :

-accroître les chances de survie à long terme de l'espèce

-ré-établir une espèce clé (au sens écologique ou culturel)

-augmenter ou maintenir la biodiversité

-apporter des bienfaits économiques à long terme à la population locale

-sensibiliser à la protection de la nature.

Une autre définition des objectifs des réintroductions/translocations est donnée par l'International Academy of Animal Welfare Sciences (1992) : il s'agit « d'établir une population viable d'une espèce dans une zone sans que cela constitue un risque physique ou sanitaire pour les populations locales humaine ou animale ».

La réhabilitation, définie comme le retour à la vie sauvage d'individus malades, blessés ou orphelins, peut également être vue comme une méthode de conservation des espèces, en particulier lorsque celles-ci sont très menacées (Kirkwood 2005).

Ces trois procédés, réintroduction, translocation et réhabilitation, font intervenir un passage plus ou moins temporaire des animaux en captivité, puis un relâcher en milieu naturel. Ainsi les considérations à prendre en compte pour la mise en place de tels programmes seront similaires.

1.2. Les besoins de la conservation

Environ 490 espèces animales connues auraient disparu ces quatre derniers siècles et l'on estime qu'en 2025, 5% à 25% des espèces connues en 1985 auront disparu (World Conservation Monitoring Centre 1992). Les espèces ne sont pas immuables et l'extinction est un processus naturel. Les taux d'extinction actuels semblent cependant beaucoup plus hauts que dans le passé et seraient causés en majorité par l'activité, directement ou indirectement (Magin *et al*. 1994). Les extinctions récentes aux causes connues seraient dues à l'introduction d'animaux (39%), la destruction d'habitat (36%), et la chasse ou l'extermination délibérée (23%) (Magin *et al*. 1994). Les mammifères seraient les plus touchés, avec 22% d'espèces globalement menacées ou éteintes (IUCN 2011). Ces chiffres ont fait naître un intérêt grandissant pour les réintroductions, translocations, et réhabilitation comme outil en biologie de la conservation, afin de sauver les espèces en déclin actuel.

La perte d'habitat augmentant avec la croissance de la population humaine et sa dépendance en ressources naturelles (Sharma 2005), les populations animales se retrouvent fragmentées et isolées. En raison de leur taille réduite et de leur isolement, ces populations courent des risques génétiques et démographiques importants (Soulé 1987). Dans les cas extrêmes, l'espèce ne se résume plus qu'à une seule population qui perd en diversité génétique, décroit fortement puis s'éteint (Soulé 1987). Ces cas extrêmes ont déjà été rencontrés avec le furet à pieds noirs (*Mustela nigripes*), le loup rouge (*Canis rufus*), le bison d'Europe (*Bison* *bonasus*), l'oryx d'Arabie (*Oryx leucoryx*), le cerf du père David (*Elaphurus davidianus*) (Magin *et al*. 1994), espèces qui se sont retrouvées éteintes dans la nature. Seal (1991) prédisait alors que les biologistes de demain seraient des « spécialistes en gestion des populations trop petites pour survivre sans l'assistance de méga-zoos ». Dans le cas des espèces citées ci-dessus, la mise en place de programme de reproduction en captivité a permis par la suite de réintroduire des individus en milieu sauvage de manière efficace (Moore & Smith 1991, Miller *et al*. 1994, Spalton *et al*. 1999, Jiang *et al*. 2000, Sipko 2009). Malgré ce succès, les programmes de reproduction en captivité font l'objet de controverses. L'antipathie face au placement en captivité, les risques d'échec des réintroductions et les coûts importants sont quelques-uns des arguments pour préférer la préservation *in situ* aux programmes de réintroduction (Seal 1991, Magin *et al*. 1994). L'idée que des zoos puissent enfin remplir réellement leur rôle dans la conservation de la nature est attrayante, mais la réalité est parfois toute autre. Lors d'une compilation des espèces de canidés captives et reproductrices, Ginsberg (1994) s'est rendu compte que la plupart des espèces se reproduisant en zoo étaient des espèces communes et que peu ou pas de programmes concernaient les espèces menacées. Nous garderons cependant à l'esprit que la réintroduction d'animaux nés en captivité est parfois préférable pour ne pas menacer les populations sauvages.

Un deuxième argument en faveur des réintroductions d'animaux captifs est plus éthique. Il concerne à la fois le problème des animaux en surplus dans les zoos, et celui des animaux blessés ou orphelins récupérés dans la nature. Pour ces derniers, les interventions se sont multipliées ces dernières décennies, soulevant un nouveau dilemme : dans quelles circonstances a-t-on le droit d'intervenir ? Kirkwood (2005) suggère de ne le faire que dans un cadre de conservation d'espèces ou pour bien-être des animaux. Avec l'amélioration des conditions de captivité, les animaux en surplus dans les zoos augmentent. Mais malgré l'intention des zoos de placer cas animaux dans la meilleure situation possible, à savoir réintroduits dans la nature, les contraintes logistiques et financières font souvent le premier obstacle (Graham 1996). D'après Kleiman & Beck (1994), la réintroduction ou translocation d'une espèce ne devrait se faire que si un ensemble de conditions sont remplies (Table 1.2).

Table 1.2: Critères pour la réintroduction/translocation : est-ce que les conditions appropriées existent ? (source : Kleiman & Beck 1994).

Condition de l'espèce
1. Besoin d'augmenter la population sauvage
2. Stock disponible
3. Pas de menace sur la population sauvage

Conditions environnementales
4. Causes du déclin supprimées
5. Habitat protégé suffisant
6. Habitat non saturé

Conditions biopolitiques
7. Pas d'impact négatif pour les locaux
8. Soutien de la communauté locale
9. Soutien d'organisations gouvernementales et non-gouvernementales
10. Conforme à la législation

Conditions biologiques
11. Technologie de la réintroduction connue ou en développement
12. Connaissance de la biologie de l'espèce
13. Ressources suffisantes pour le programme

Réintroduction/translocation recommandée ?

Peu d'espèces pour lesquelles un programme de réintroduction existe ou a été imaginé rempliraient toutes ces conditions. Pourtant, le besoin semble réel et la communauté scientifique s'est donc intéressée à la biologie de la conservation, encore mal reconnue comme véritable discipline scientifique (Stem *et al*. 2005). L'événement le plus notable est sans doute la création par l'UICN d'un groupe de spécialistes de la réintroduction (Reintroduction Specialist Group, RSG) au début des années 1990. La notion de replacer des espèces dans des zones où elles avaient disparu n'est pas nouvelle. Le grand tétra (*Tetrao urogallus*) a par exemple été réintroduit en Ecosse en 1837 (Stuart 1991). Mais durant de nombreuses années, les tentatives étaient menées de manière hasardeuse, par des individus dévoués, procédant à tâtons, résultant en un grand nombre d'échecs (Robinson 2005). Les nombreux échecs montrent que la discipline en est encore à ses débuts et qu'il est nécessaire d'apprendre des expériences passées (Seddon *et a*l. 2007, Gusset 2009).

1.3. Etude de cas

Plusieurs revues des programmes de réintroduction et de translocation ont été publiées, entre autre pour évaluer le succès des différents programmes et faire des recommandations (Beck *et al*. 1994, Reading & Clark 1996, Fischer & Lindenmayer 2000, Breitenmoser *et al*. 2001, Sharma 2005). Je présenterai quelques résultats sur les programmes de réintroduction toutes espèces de mammifères confondues, avant de me concentrer sur les carnivores dont le danger potentiel envers l'homme et son bétail en fait un sujet délicat.

Comme nous venons de le voir, la réintroduction est une discipline encore en développement et le besoin s'est vite fait ressentir de collecter un maximum d'informations sur les méthodes utilisées par les uns et les autres afin d'identifier les raisons des succès et échecs et pour éviter de reproduire les mêmes erreurs ou des méthodes inefficaces. Beck *et al*. (1994) se sont intéressés à 46 programmes de réintroduction de 39 espèces mammifères issus de la captivité et les ont recensé sur 10 caractéristiques a priori pertinentes pour le succès de tels projets (Table 1.3).

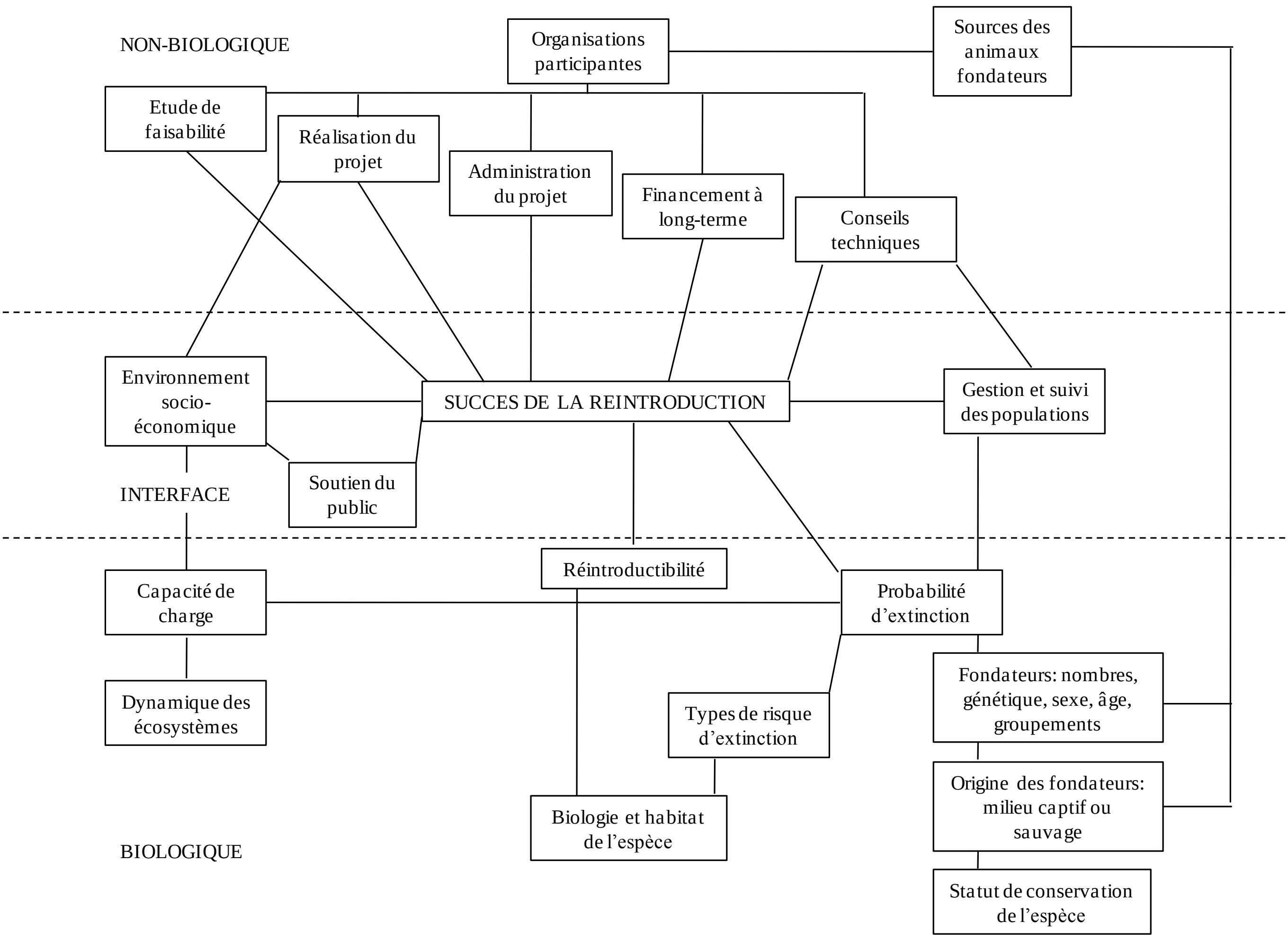
Table 1.3: Caractéristiques de programmes de réintroduction de mammifères (46 projets pour 39 espèces, définitions : voir texte) (source : Beck *et al*. 1994).

Caractéristique étudiée	**Proportion des projets**
Entraînement pré-relâcher	36%
Acclimatation	83%
Dépistage médical	60%
Dépistage génétique	35%
Entraînement post-relâcher	12%
Approvisionnement	69%
Monitoring	97%
Embauche locale	50%
Stages professionnels	52%
Education de la communauté locale	59%

L'entraînement pré-relâcher inclut des mesures telles qu'inciter le tamarin lion doré (*Leontopithecus rosalia*) à chercher de la nourriture cachée et distribuée dans l'espace, ainsi qu'à se déplacer dans l'environnement naturel de sa cage (Beck *et al*. 1991), ou encore inciter le furet à pieds noirs à trouver et tuer des chiens de prairie (*Cynomys ludovicianus*) dans de grands enclos extérieurs (Miller *et al*.1994). L'acclimatation signifie que les individus ont été gardés au moins 24 heures avant le relâcher dans des cages ou enclos sur le site de relâcher, afin de se familiariser avec les conditions climatiques, le terrain et la nourriture du milieu. Le dépistage médical suppose que la sélection des candidats à la réintroduction s'est faite au moins en partie sur des considérations médicales. Les loups rouges (*Canis rufus*) ont par exemple été vaccinés contre la rage, la maladie de Carré, la parvovirose, l'hépatite, la leptospirose, le coronavirus et la para-influenza (Phillips 1990). Lors du dépistage génétique, la sélection des candidats s'est faite au moins en partie sur des considérations génétiques. Pour l'oryx d'Arabie, on s'est assuré que les individus soient suffisamment éloignés génétiquement pour éviter la consanguinité des générations futures (Spalton 1991). L'entraînement post-relâcher consiste par exemple à montrer aux chimpanzés (*Pan troglodytes*) relâchés la collecte de nourriture et la construction de nids (Carter 1981). L'approvisionnement signifie qu'eau, nourriture et/ou abri étaient à la disposition des individus relâchés. Le monitoring inclut le suivi de la taille de la population réintroduite, du décompte des naissances, des causes de mortalités, etc. Cela peut se faire par observation directe, télémétrie ou récolte d'indices (excréments, restes de proies, etc.). L'identification des individus par tatouage, transpondeur, oreillette ou marque corporelle facilite le monitoring. L'embauche locale signifie que des salaires ont été versés à du personnel sur place en échange de travaux, tels que la construction d'enclos par exemple. Le programme a offert des stages professionnels si des étudiants diplômés ont poursuivi des recherches directement en lien avec le programme de réintroduction. L'éducation de la communauté locale inclut conférences, posters, distributions de T-shirt, visites scolaires, événements culturels et communication dans les médias.

Plusieurs points ressortent dès à présent de cette revue : (1) la réintroduction ne fait pas qu'intervenir la biologie, mais une multitude de disciplines, en particulier liées au facteur humain ; (2) la réintroduction doit être envisagée sur le long-terme, d'où l'importance de former du personnel ; (3) un certain nombre de critères dans le choix des animaux, des méthodes et des sites semblent être primordiaux et doivent être étudiés plus en profondeur (Fig 1.1).

Fig 1.1: Facteurs pertinents dans le succès des réintroductions (source : Stanley Price 1991).



La revue des projets de réintroduction passés, en cours, et suggérés par l'UICN (Table 1.4) donne un aperçu des espèces majoritairement concernées, de la localisation des projets et des méthodes utilisées.

Table 1.4: Liste des projets de réintroduction passés, en cours et proposés (source : Wilson & Stanley Price 1994).

Espèce	Pays	Statut	Origine des animaux	Cause du déclin
Marsupiaux				
Bettongia lesueur	Australie	R	sauv	3/5
Bettongia penicillata	Australie	E	cap	3/5
Lagorchestes hirsutus	Australie	R	cap	3/5
Phascogale tapoatafa	Australie		cap	3/5
Parameles gunnii	Australie		sauv	3/5
Petaurus breviceps	Australie			3/5
Macrotis lagotis	Australie	E		3/5
Myrmecobius fasciatus	Australie	E	cap+ sauv	3/5
Primates				
Varecia varecia	Madagascar	V	cap	
Ateles geoffroyi	Panama	V	sauv	
Leontopithecus rosalia	Brésil	E		
Macaca sylvanus	Maroc	V	cap	1/5
Macaca silenus	Inde	E		
Pongo pygmaeus	Indonésie	E		1
Rongeurs				
Sciurus vulgaris	Royaume-Uni			3/5
Leporillus conditor	Australie	R	cap	
Geocapromys brownii	Jamaïque	I	cap	
Muscardinus avellanarius	Royaume-Uni			
Carnivores				
Canis lupus	Etats-Unis	V	sauv	1
Canis rufus	Etats-Unis	E	cap	1/3/5
Lycaon pictus	Afrique du Sud	E	sauv	1
Lycaon pictus	Namibie	E		1
Vulpes velox	Canada		cap+ sauv	
Lutra canadensis	Etats-Unis		sauv	
Lutra lutra	Royaume-Uni	V	cap	1/2/5
Enhydra lutris	Etats-Unis/Canada		sauv	1
Mustela nigripes	Etats-Unis	Ex	cap	1/3/5
Acionyx jubatus	Afrique du Sud	V	sauv	1/5
Lynx lynx	Suisse		sauv	1/5
Lynx lynx	France		sauv	1/5
Lynx canadensis	Etats-Unis		sauv	1
Lynx pardinus	Espagne/Portugal	E	sauv	1/5
Ailuropoda melanoleuca	Chine	E	cap	1/5
Périssodactyles				
Equus hemionus	Israël		cap	1/3/5
Equus hemionus	Arabie Saoudite		cap	1/3/5
Equus przewalskii	Russie	Ex	cap	1/3/5
Equus przewalskii	Mongolie	Ex	cap	1/3/5
Equus przewalskii	Chine	Ex	cap	1/3/5
Rhinoceros unicornis	Inde	E	cap	1/5
Artiodactyles				
Cervus elaphus	Algérie	V	cap	1
Cervus nippon	Taiwan	E	cap	1/5

Elaphurus davidianus	Chine	E		1/5
Hippocamelus bisculeus	Chili	E	cap+sauv	
Capreolus capreolus	Israël		cap	1/3/5
Antilope cervicarpa	Pakistan		cap	
Rangifer tarandus	Etats-Unis/Canada		sauv	
Alces alces	Etats-Unis		sauv	
Bison bonasus	Pologne/Russie	V	cap	1/5
Addax nasomaculatus	Tunisie	E	cap	1/5
Addax nasomaculatus	Niger	E	cap	1/5
Gazella cuvieri	Algérie	E	cap	1/5
Gazella gazella	Arabie Saoudite	E	cap	1/5
Gazella dama	Sénégal	E	cap	1
Gazella subgutterosa	Arabie Saoudite		cap	1
Oryx leucoryx	Oman	E	cap	1
Oryx leucoryx	Jordanie	E	cap	1/5
Oryx leucoryx	Israël	E	cap	1/5
Oryx dammah	Tunisie	E	cap	1
Rupicapra pyrenaica	Italie	V	cap	1/5
Capra ibex	Jordanie		cap	1/5
Ovis canadensis	Etats-Unis		cap	1

(Statut : catégories des auteurs: Ex=éteint dans la nature ; E=en danger ; V=vulnérable ; R=rare. Origine des animaux : cap=captivité ; sauv=sauvage. Cause du déclin : 1=chasse ; 2=pollution ; 3=compétition, prédation ; 4=fragmentation des populations ; 5=perte d'habitat).

D'après ces données, 24% des projets concernent des carnivores, et parmi eux 73% se situent en Europe et Amérique du Nord. Breitenmoser *et al*. (2001) rapporte que la réintroduction de carnivores n'est devenue envisageable qu'au milieu du 20ème siècle, lorsque l'attitude générale envers les prédateurs changea. Le premier programme de réintroduction date de 1941 et concernait le lynx (*Lynx lynx*) en Russie (Breitenmoser *et al*. 2001). Les carnivores, et en particulier les grands prédateurs, sont en perpétuel conflit avec l'homme et leur réintroduction provoque souvent des controverses vivement et longuement débattues. Pourquoi alors réintroduire ces animaux si ce n'est pour sauver des espèces menacées ? La plupart des programmes de réintroduction de carnivores concernent pourtant des espèces communes et répandues, avec quelques exceptions d'espèces menacées (Breitenmoser *et al*. 2001). Les auteurs affirment que l'homme a pris conscience de l'importance des carnivores dans les écosystèmes et de sa mise en cause dans leur extinction passée. On peut également avancer l'hypothèse de l'expérience. Les réintroductions peuvent être testées sur des espèces relativement communes, pour utiliser par la suite les méthodes avec des espèces proches menacées (Robinson 2005).

En ce qui concerne les canidés, d'après le groupe de spécialistes de l'UICN (IUCN/SSC Canid Specialist Group 2004), sur les 37 taxa que comptent les canidés :

- 1 est éteint (EX)
- 3 sont en danger critique d'extinction (CR)

- 3 sont en danger (EN)
- 3 sont vulnérables (VU)
- 1 est quasi-menacé (NT)
- 20 sont à préoccupation mineure (LC)
- 6 ont un statut inconnu car les données sont insuffisantes (DD).

J'ai compilé 24 programmes de réintroduction concernant 6 espèces de canidés (Table 1.5), puis ai rapporté leur résussité (échec/succès) en fonction de leurs caractéristiques (Fig 1.2).

Table 1.5: Liste des programmes de réintroduction concernant les canidés, et leurs caractéristiques.

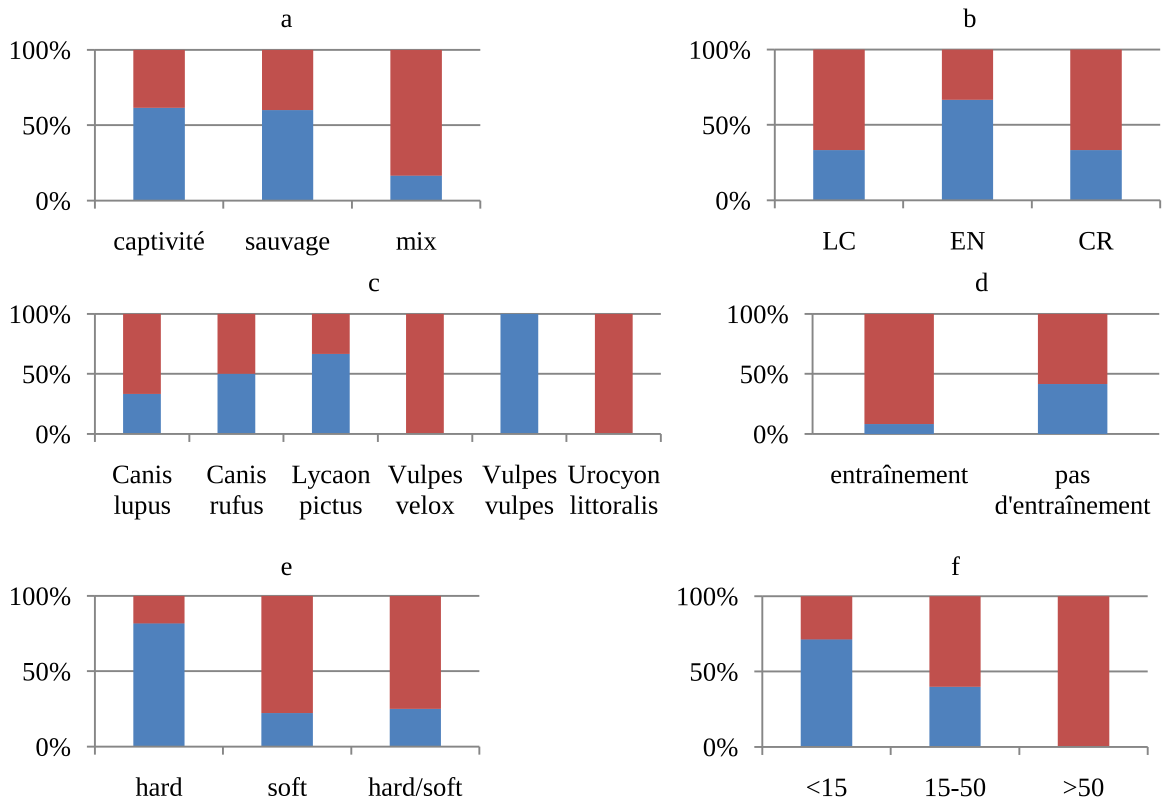
Espèce	**St**	**Pays**	**Années**	**Origine**	**Nb**	**Ent**	**Relâcher**	**Succès**	**Référence**
Loup gris (*Canis lupus*)	LC	Etats-Unis (Alaska)	1972	captivité	5	non	hard	échec	Henshaw *et al*. 1979
Loup gris (*Canis lupus*)	LC	Etats-Unis (Michigan)	1974	sauvage	4	non	hard	échec	Reading & Clark 1996
Loup gris (*Canis lupus*)	LC	Géorgie	1974-1979	captivité	22	oui	soft	succès	Badridze 1999
Loup gris (*Canis lupus*)	LC	Etats-Unis (Minnesota)	1975-1978	sauvage	107	non	hard	succès	Fritts et al. 1984
Loup gris (*Canis lupus*)	LC	Etats-Unis (Idaho)	1995-1996	sauvage	84	non	hard/soft	succès	Fritts *et al*. 1995
Loup du Mexique (*Canis l. baileyi*)	LC	Etats-Unis (Arizona)	1998	captivité	11	oui	hard/soft	succès	Parsons 1998
Loup rouge (*Canis rufus*)	CR	Etats-Unis (Caroline du Nord)	1987-1995	captivité	69	oui	soft	succès	Phillips 1992
Loup rouge (*Canis rufus*)	CR	Etats-Unis (Tenessee)	1991-1992	captivité	37	oui	soft	échec	Kelly *et al*. 2008
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1975	sauvage	5	non	hard	échec	Lines 2003
Lycaon (*Lycaon pictus*)	EN	Namibie	1978	captivité	6	non	hard	échec	Scheepers & Venzke 1995
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1980-1981	mix	24	non	soft	succès	Maddock 1999
Lycaon (*Lycaon pictus*)	EN	Zimbabwe	1986	captivité	9	non	hard	échec	Lines 2003
Lycaon (*Lycaon pictus*)	EN	Namibie	1989	captivité	5	non	hard	échec	Scheepers & Venzke 1995
Lycaon (*Lycaon pictus*)	EN	Namibie	1990	captivité	13	non	hard	échec	Scheepers & Venzke 1995
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1991	captivité	8	non	soft	échec	Lines 2003
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1992	sauvage	14	non	hard	échec	Lines 2003
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1995	mix	6	non	soft	succès	Lines 2003
Lycaon (*Lycaon pictus*)	EN	Kenya	1997	mix	6	non	hard	échec	Kock *et al*. 1999
Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	1999	mix	9	non	soft	succès	van Dyk & Slotow 2003

Lycaon (*Lycaon pictus*)	EN	Afrique du Sud	2001	mix	5	non	soft	succès	Lines 2003
Renard véloce (*Vulpes velox*)	LC	Canada (Alberta)	1978-1997	mix	942	oui	hard/soft	succès	Bremner & Cypher 2007
Renard véloce (*Vulpes velox*)	LC	Etats-Unis (Montana)	1998-2002	captivité	117	oui	soft	succès	Bremner & Cypher 2007
Renard roux (*Vulpes vulpes*)	LC	Royaume-Uni	1992	captivité	26	non	hard/soft	échec	Robertson & Harris 1995
Renard gris insulaire (*Urocyon littoralis*)	CR	Etats-Unis (Californie)	2003-2004	captivité	23	non	hard	succès	Bremner & Cypher 2007

(St=statut : catégories de l'UICN, voir plus haut ; Nb=nombre d'individus relâchés ; Ent=entraînement)

Fig 1.2: Réussite (échec/succès) des 24 programmes de réintroduction de canidés rangés par caratéristiques

(a. origine des animaux relâchés ; b. statut des espèces concernées ; c. espèces concernées ; d. entraînement avant relâcher ou non ; e. relâcher *hard/soft* ; f. nombre d'individus relâchés).



D'après les résultats de cette compilation, l'origine captive ou sauvage des individus relâchés n'influence pas vraiment la réussite de la réintroduction, mais la meilleure option semble être un mélange des deux : des individus issus à la fois de la captivité et du milieu sauvage. Les programmes de réintroduction des espèces à préoccupation mineure et en danger critique d'extinction ont eu plus de réussite que ceux des espèces en danger. Les programmes qui

entraînent les individus avant le relâcher ont plus de succès que ceux qui ne les entraînent pas. Le relâcher soft ou une utlisation des deux types de relâcher engendrent une meilleure réussite des réintroductions. Le nombre d'individus relâchés influence la probabilité de succès : les programmes qui ont relâché moins d'une quinzaine d'individus ont essuyé beaucoup d'échecs alors que les programmes qui ont relâché plus de 50 individus ont tous réussi (Fig 1.2).
Ainsi les expériences passées de réintroduction de canidés montrent certaines tendances que la rechercher future se devra d'éclaircir pour améliorer le succès des réintroductions. En étudiant le relâcher expérimental de loups gris en Russie, cette thèse participera aux besoins de la recherche en biologie de la conservation.

1.4. Contexte de l'étude

La chasse est très populaire en Russie, que ce soit pour se nourrir ou pour les trophées. La chasse à l'ours est pratiquée à ces deux fins dans toute la Russie. Jusqu'à récemment, la saison de chasse s'ouvrait en janvier, lorsque les ours sont en hibernation, période où les femelles mettent bas. La chasse à la tanière laisse des oursons orphelins voués à la mort (froid, faim). Environ 2000 ours vivent dans la région de Tver (84 000 km^2) située entre Moscou et Saint-Pétersbourg. Le quota de chasse est fixé à 10% de la population, soit environ 200 ours (Pazhetnov & Pazhetnov 2005). Les données officielles rapportent environ 170 ours tués légalement, auxquels il faut ajouter pas moins de 70 ours braconnés chaque année. La population n'est pas menacée, mais cette chasse résulte en une douzaine d'oursons orphelins chaque année, qui sont destinés à mourir, à finir leur vie en captivité ou à être exhibés dans des cirques (Pazhetnov & Pazhetnov 2005). En 1976, en partenariat avec la réserve Tsentralno-Lesnoy Zapovednik, Dr. Valentin Pazhetnov créé la Station Biologique « Chisty Les » (district de Toropets, région de Tver, Fédération de Russie) pour sauver les oursons orphelins (Fig 1.2). Depuis cette date, plus de 100 oursons ont été élevés et relâchés dans la nature. Le point-clé de la méthode semble se situer dans le minimum de contacts humains entre les ours et l'homme. En particulier, lors du nourrissage au biberon pour les plus jeunes, le personnel ne doit pas parler, doit porter des gants et des masques sombres afin de couvrir les parties brillantes et donc remarquables. Le but est de minimiser la possibilité pour un ourson de faire le lien entre la nourriture et n'importe quel stimulus externe qui serait suffisamment distinctif et reconnaissable (Pazhetnov & Pazhetnov 2005).

Fig 1.3: La réserve Tsentralno-Lesnoy Zapovednik et la Station Biologique « Chisty Les » dans la région de Tver, Fédération de Russie.

La chasse au loup est pratiquée dans un contexte un peu différent. L'animal a le statut de nuisible et sa chasse est autorisée tout au long de l'année par n'importe quel moyen. De plus, une prime de 1500 roubles (40 €) est promise pour chaque loup tué. La chasse à la tanière représente 10% des loups tués et constitue la deuxième technique la plus utilisée après le fladry (Becker 2006). Les louveteaux sont prélevés dans la tanière, puis tués ou revendus. En

1993, alors biologiste à la réserve Tsentralno-Lesnoy Zapovednik, Vladimir Bologov se voit confié un louveteau orphelin provenant de la chasse. Sur les conseils du Dr. Valentin Pazhetnov, il étudiera de près le comportement de cet animal, pour déterminer les étapes importantes dans le développement des aptitudes à se déplacer, se nourrir et se défendre, d'un individu élevé sans parents. Par la suite, Vladimir Bologov créé le centre de réhabilitation de louveteaux orphelins à la Station Biologique « Chisty Les », où 64 loups ont été recueillis depuis 1993. Le programme de réintroduction du loup en Russie a été présenté pour la première fois à la communauté scientifique au World Wolf Congress en 2003 (Bologov & Ovsyanikov 2003), avec des premiers résultats encourageants.

1.5. Objectifs de recherche

Tout au long de cette introduction, nous avons vu que les réintroductions, translocations et réhabilitations sont des processus complexes, de longue haleine, qui débouchent souvent sur des échecs. Pourtant, nous avons également vu l'intérêt grandissant pour ces méthodes en biologie de la conservation. La présente recherche a donc eu pour objectif de montrer la réussite du relâcher expérimental de loups élevés en captivité afin de défendre l'hypothèse que la réintroduction d'animaux captifs est une pratique envisageable, même pour des grands prédateurs potentiellement dangereux pour l'homme et son bétail. J'ai étudié 64 loups et analysé leurs comportements lors de la captivité et une fois relâchés, afin d'évaluer leurs aptitudes à survivre en milieu naturel. Parallèlement, j'ai testé la prédictibilité des sites de relâcher et la performance du suivi satellitaire, deux points clés dans le processus de réintroduction

Cette thèse est organisée en cinq chapitres principaux, chacun des chapitres traitant de considération à prendre en compte lors du relâcher d'animaux captifs. Le chapitre 2 s'intéresse aux traits comportementaux d'individus relâchés, pour trouver un moyen d'évaluation efficace et fiable, déterminer les groupes de traits comportementaux importants dans la sélection de candidats au relâcher et estimer l'influence de différents facteurs environnementaux et sociaux sur ces comportements. Le chapitre 3 donne les premiers résultats du suivi post-relâcher de six loups, analyse les déplacements de chaque individu et se penche sur les différences entre relâchers avec et sans site d'acclimatation. Dans le chapitre 4, j'ai analysé les excréments de loups relâchés afin de déterminer leur régime alimentaire et sa variation au cours des saisons. Dans le chapitre 5, j'ai testé la performance de deux modèles de collier GPS pour comparer leur efficacité dans le cadre du suivi de loups en taïga russe. Le chapitre 6 évalue les variables déterminantes pour l'habitat du loup afin de prédire la localisation de sites de relâcher.

Chaque chapitre de cette thèse correspond à une publication scientifique.

2) L. Becker, A. Ancel, V.V. Bologov. *Behavioural trait assessment of captive-raised wolves for rehabilitation programme.* (en preparation).
3) L. Becker, V.V. Bologov, A. Ancel, J.A. Hernandez-Blanco, M.D. Chistopolova, A.D. Poyarkov, V.V. Rozhnov. *Early post-release movements of reintroduced wolves in Russia.* (en preparation).
4) L. Becker, A. Ancel, C. Choquel, H. Le Berre, V.V. Bologov. *Evaluation of two GPS telemetry collars performance for wolf monitoring in the boreal forest.* Wildlife biology (soumis).
5) L. Becker, A. Ancel, V.V. Bologov. *Habitat evaluation for grey wolves in Tver region, Russian Federation.* (en preparation).
6) L. Becker, A. Ancel, L. Bourg, C. Fraissard, V.V. Bologov. *Food habits of captive-raised wolves reintroduced into the wild*. Acta Theriologica (soumis).

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Chapter 2. Behavioural trait assessment of captive-raised wolves for rehabilitation programme

Chapitre 2. Evaluation des traits comportementaux de loups élevés en captivité et destinés à la réhabilitation

Глава 2. Оценка поведенческих черт волков выращенных в неволе и предназначенных для реабилитации

2.1. Abstract

Abstract: In reintroduction programmes, candidates are usually selected on basic criteria such as age, sex and health, whereas previous recommendations have highlighted the importance of behavioural skills required, in particular locomotion and food acquisition. The recent research in behavioural variation have demonstrated that individuals differ in their way to cope with the situations, but which behavioural traits would be relevant to the survival of released animals remained poorly investigated. Individual behavioural variation of 57 wolves was assessed using observers' ratings on 21 behavioural traits. Inter-rater agreement was high for most questionnaire items and individuals rated. Principal component analysis suggested that the traits affiliative-bold, warm-friendly and eccentric-playful explained about 65% of the total variance. Early experiences, such as age of separation from the pack and raising method, seem to play an important role in shaping an individual's tendencies to be confident and affiliative or fearful and timid. Comparisons with previous research show evidence for a cross-species generality in the components boldness, sociability, playfulness and aggressiveness. Assessment of individual behavioral variation through questionnaire ratings

may therefore provide a simple and non-invasive tool for predicting an individual's ability to be released and survive in the wild.
Key words: *Canis lupus,* animal personality, individual behavioural variation, release criteria.

Résumé : Dans les programmes de réintroduction, les candidats sont généralement sélectionnés sur des critères de base tels que : âge, sexe et état sanitaire. Pourtant des recommandations antérieures ont souligné l'importance de s'assurer que les candidats présentent aptitudes comportementales requises, en particulier en ce qui concerne la locomotion et la recherche de nourriture. Les récentes recherché sur la variation comportementale ont démontré que les individus avaient des façons différentes de gérer les situations. Mais l'identification des traits comportementaux pertinents pour la survie d'animaux relâchés reste peu étudiée. La variation comportementale individuelle de 57 loups a été évaluée à l'aide de notation d'observateurs sur 21 traits comportementaux. L'accord entre juges était fort pour la plupart des questions de l'enquête et pour la majorité des individus notés. Une analyse en composantes principales a fait ressortir que les traits attaché-audacieux, affectueux-amical et excentrique-joueur expliquaient environ 65% de la variabilité totale. Les expériences précoces, telles que l'âge de séparation de la meute et la méthode d'élevage, semblent jouer un rôle important dans le développement des tendances des individus à être confiant et attaché ou peureux et timide. La comparaison avec des études précédentes montre une certaine généralité entre espèces pour les composantes : audace, sociabilité, jeu et agressivité. L'évaluation de la variation comportementale entre individus par notation sur questionnaire peut donc fournir un outil simple et non-invasif pour prédire l'aptitude d'un individu à être relâché et survivre dans la nature.
Mots-clés : *Canis lupus*, personnalité animale, variation comportementale individuelle, critères de relâcher.

Абстракт: Кандидаты для программ реинтродукций обычно отбираются по таким основным критериям, как возраст, пол и состояние здоровья. Однако предыдущие рекомендации подчеркнули необходимость убедиться в том, что кандидаты имеют требуемые навыки поведения, в частности, в отношении передвижения и поиска пищи. Недавнее исследование поведенческих вариаций продемонстрировало, что индивиды различаются по их способности справляться с конкретными ситуациями. Однако вопрос о том, какие именно поведенческие черты имеют отношение к выживанию выпущенных животных, остается мало изученным. Индивидуальные вариации

поведения 57 волков было оценены при помощи оценок наблюдателей по 21 поведенческой черте. Наблюдатели были во многом согласны по большинству пунктов анкетного опроса и в отношении большинства исследуемых индивидов. Анализ основных компонентов показал, что черты товарищески-смелый, ласково-дружеский и эксцентрично-игривый могут объяснить приблизительно 65 % общей изменчивости. Такой ранний жизненный опыт, как возраст отделения от стаи и метод выращивания, вероятно играет важную роль в формировании тенденций индивидов проявлять либо уверенность и аффилиативное поведение, либо быть пугливыми и робкими. Сравнения с предыдущими исследованиями показывают определенную межвидовую общность по компонентам: смелость, общительность, игривость и агрессивность. Оценка индивидуальных поведенческих вариаций при помощи анкеты может служить простым и неинвазивным способом предсказания способности индивида быть выпущенным и выжить в дикой природе.
Ключевые слова: *Canis lupus*, индивидуальность животных, индивидуальная поведенческая вариация, критерии выпуска.

2.2. Introduction

Restoring extirpated species to their natural environment is not new, but has been hidden by the more successful wild-to-wild translocations (Griffith *et al*. 1990). In some cases however, the use of captive-bred animals is preferable, because translocations could endanger the remaining wild population (Wilson & Stanley Price 1994). During the last decades, the interest for the science of reintroduction has increased, due to the need for zoos to play a more active role in the conservation species and to deal with their surplus animals (Graham 1996). The creation of a Reintroduction Specialist Group (RSG) by the International Union for Conservation of Nature / Species Survival Commission (IUCN/SSC) reflects this interest. In their guidelines (UICN 1998), they advise that the release stock (1) is closely related genetically to the original native stock, (2) does not endanger the captive stock population, (3) must be subjected to veterinary screening, (4) should be given the opportunity to learn for their survival, and (5) must not be confident in the presence of humans.

In many reintroduction programmes, the selection of release candidates is only based on age, sex and health (Yalden 1993). Previous recommendations for candidate selection have highlighted the importance of behavioural skills required, in particular locomotion and food acquisition (Kleiman 1989). Captivity may have great effects on the behaviour of wild mammals including influences on the genetics of a captive population, on the development of behaviour, and on the psychology of confined mammals (Carlstead 1996). Release stock of captive animals thus needs monitoring to ensure that captivity did not degrade their behavioural skills required for survival. In a review on the effects of captive experience on reintroduction survival in carnivores, Jule *et al.* (2008) found that (1) wild-caught carnivores were significantly more likely to survive than captive-born carnivores in reintroductions; (2) that humans were the direct cause of death in over 50% of all fatalities; and (3) that reintroduced captive-born carnivores were particularly susceptible to starvation, unsuccessful predator/competitor avoidance and disease. For example, released captive-bred African wild dogs (*Lycaon pictus*), showed a lack of hunting skills and human avoidance (Woodroffe & Ginsberg 1999); released wolves (*Canis lupus*) in Alaska, as well, were ineffective hunters and approached humans (Henshaw *et al*. 1979).

In recent years, increasing number of studies on variation in behaviour among non-human individuals (Clark & Ehlinger 1987, Bolig *et al*. 1992, Mather & Anderson 1993, Hansen 1996, Coleman & Wilson 1998, Mettke-Hofmann *et al*. 2005) have demonstrated that individuals differ in their behaviour in a consistent manner, and that this variation may significantly affect the way individuals interact with the environment (McDougall *et al*. 2005). The concept of “temperament” refers to this consistency of character over time and across contexts (Clark & Ehlinger 1987, Wilson *et al*. 1994, Dingemanse *et al*. 2002, McDougall *et al*. 2005). Temperament can be described by a series of traits that usually include activity, tameness, aggressiveness, exploration, sociability and boldness (Gosling 2001). Variation in temperament can lead to individual differences in behavioural patterns relevant to captivity or reintroduction. The effects of behavioural variation on the welfare and management of animals have been studied in farms (Spoolder *et al*. 1996, Wemelsfelder *et al*. 2000) and zoos (Dutton *et al*. 1997, Carlstead 1999, Wielebnowski 1999), to assess the suitability of individuals for a particular requirement: human consumption, captive breeding, exhibition, etc. But McDougall *et al*. (2005) admitted that our current knowledge is limited as to which temperament traits are the most important for the survival of newly reintroduced individuals.

One component of personality that has recently been discussed as potentially significant in terms of natural selection is boldness. Variation in fearfulness, boldness and shyness is a fundamental element in human personality (Wilson *et al*. 1994) and some studies have shown similar variation in various animals: cats (Lowe & Bradshaw 2001), ungulates (Lyons *et al*. 1988, Réale *et al*. 2000), canids (Fox 1972, Harri *et al*. 1995, Bremner-Harrison *et al*. 2004), fish (Huntingford & Giles 1987, Coleman & Wilson 1998, Ward *et al*. 2004) and octopus (Mather & Anderson 1993). Individual variation in boldness/shyness may have important implications for survival of released animals. In a recent study, Bremner-Harrison *et al*. (2004) demonstrated that reintroduced swift fox that died following release were those with high levels of boldness. This example shows the importance of behaviour evaluation in reintroduction programme and the need to investigate which traits are required.

The goal of this study is to provide a method for assessing individual behavioural variation in captive wolves in the frame of a reintroduction programme. We used observer questionnaires to obtain ratings on 21 behavioural items including general behaviour, social behaviour and wolf-human behaviour, of 57 wolves. Patterns in behavioral variation obtained from the questionnaire results were identified using principal component analysis. Individual scores were then examined with regard to gender, raising method, caging conditions and human contact. We hope to identify environmental and social variables that impact on wolf behaviour, and to identify behavioural traits that distinguish potentially successful individuals than less successful individuals for reintroduction.

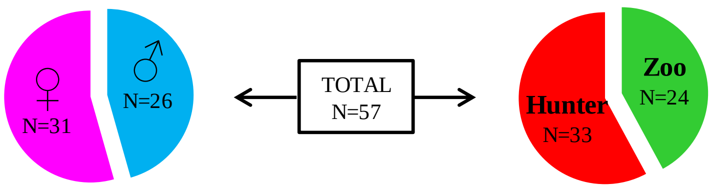
2.3. Material and methods

2.3.1. Study animals and facilities

Fifty-seven captive-raised wolf pups were the subjects of this study. There were 31 females and 26 males; 33 were wild-born and 24 captive-born (Fig 2.1).

The wolves came from hunters (from the regions of Bashkiria, Pskov, Smolensk, Tver and Udmurtia), and from zoos (Belgorod, Nijni-Novgorod, Saint-Petersburg, Tambov, Veliki Ustiug and Yaroslavl). They were raised in one of the 4 wolf enclosures of the Biological Station “Chisty Les” (Toropets district, Tver region, Russian Federation). Enclosures were 700 to 15000 m^2, made of fence surrounding a piece of unspoiled forest, and located far away from human settlements (about 1.5 km from first inhabited village). Some wolves were free during the day and closed in enclosure for the night (‘tutor’ raising method). Wolves arrived at the rehabilitation centre between 2 and 17 weeks old, and stayed there for several months before they were released to the wild. They were provided with food 2-3 times per week, with average amount of 1kg/wolf/day. The food provided was mainly meat from the slaughterhouse (chicken, pork, beef and horse), road kills (hare, birds), remains of hunting (wild boar, moose) or fish (whiting, cod, pout). Water was provided *ad libitum*.

Fig 2.1: Sex composition and origin of the 57 studied wolves.



For every wolf, we reported gender, origin (hunter/zoo), age of separation from the pack and the following criteria about their social and environmental caging (Table 2.1).

Table 2.1: Definitions and classifications of social and environmental criteria.

Category	Definitions
Raising method	*Tutor*: raised in enclosure with siblings only. The wolves are free during the day and follow the human tutor. *Feeder*: raised in enclosure with siblings only. Human come for observing and feeding. *Foster*: raised in enclosure with one or several foster adult wolves. Human come for observing and feeding.
Human contacts	*Few*: contact with 1-5 different humans. *Many*: contact with many different humans (more than 10).
Human frequency	*Daily*: Human came to the enclosure about once per day. *Weekly*: Human came to the enclosure about once per week.

2.3.2. Observer questionnaire

Twenty-one behavioral adjectives were chosen as items for assessment of individual behavioral variation (Table 2.2). Questionnaire was based on adjectives used in previous studies with domestic cats (*Felis catus*) (Feaver *et al*. 1986), rhesus monkeys (*Macaca mulatta*) (Stevenson-Hinde & Zunz 1978), chimpanzees (*Pan troglodytes*) (Buirski & Plutchik 1991), spotted hyenas (*Crocuta crocuta*) (Gosling 1998), horses (*Equus caballus*) (Mills 1998), and cheetahs (*Acinonyx jubatus*) (Wielebnowski 1999). However, we made some changes to adapt the items for rating wolf behaviour.

Three observers (Laetitia Becker, Ekaterina Blidchenko and Vladimir Bologov) rated individual wolves. Twelve wolves were rated by all 3 observers (Fig 2.2). Observers had worked with wolves for minimum 3 months. Before rating, the observers only discussed the rating procedure and the definitions of given adjectives, and they made their ratings independently. They were asked to base their ratings on the full length of their experience with the wolves.

The rating method was identical to the one used by Gosling (1998). Ratings were made on a 5-point scale ranging from *extremely uncharacteristic* (1) to *extremely characteristic* (5), (3) representing *in between, neutral*. Observers were encouraged to use the full range of the scale.

Fig 2.2: Scheme of the 57 wolves rated by the 3 observers.

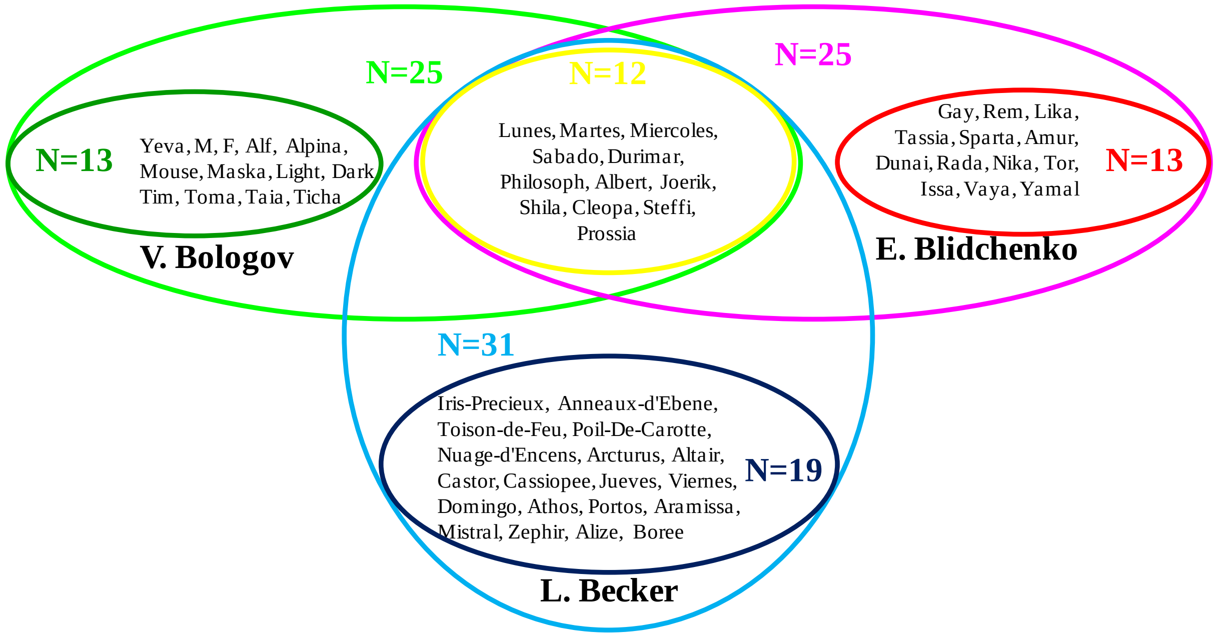


Table 2.2: Behavioral definitions of adjectives used for questionnaire ratings.

Category 1 (general wolf behaviour)	
Active	Moves about a lot, distance travelled by walking, running, climbing, or jumping. Not lethargic.
Bold	Behaves in a positive, assured manner. Exhibits courage in the face of danger. Is daring, not restrained or tentative. Not timid, shy, or coy.
Calm	Not easily disturbed, not agitated. Restful, peaceful.
Confident	Self-assured, certain, self-reliant. Does not hesitate to act alone; does not seek reassurance from others.
Curious	Readily approaches and explores changes in the environment. Appears to be interested in new situations.
Eccentric	Shows stereotypic or abnormal behaviours.
Fearful	Hesitant, indecisive, tentative, afraid. Fears and avoids any kind of risk, shows change in posture and movements. Exhibits a defensive reaction in anticipation of a dangerous stimulus. Overly alarmed, retreats readily from others or from outside disturbances, a reaction, generally excessive, to actual or potential danger or threats.
Greedy	Is greedy. Has a keen, excessive appetite; ravenous. Is gluttonous, devouring. Rapacious.

Imaginative	Approaches situations in novel, creative ways; for example, finds many ways to escape.
Moody	Displays frequent mood swings. Not predictable, patterned, or steady.
Playful	Wrestling, chasing with exaggerated movements, and rapid shifting of roles, initiates play and joins in when play is solicited.
Smart	Learns quickly to associate certain events and appears to remember for a long time.
Vigilant	Ready, attentive, watchful, notices with special attention. Not oblivious to surroundings.
Vocal	Frequently vocalizes.
Category 2 (social wolf behaviour)	
Aggressive	Frequently reacts hostile (e.g., attacks, growls) toward another group member.
Friendly	Friendly, amicable, and congenial toward other animals. Responds to others in an easy, kind, manner. Not hostile. Not antagonistic.
Sociable	Seeks companionship/company of others, prefers not to spend time alone.
Warm	Seeks bodily closeness, touching, grooming; for example, one animal lying on another.
Category 3 (wolf-human behaviour)	
Hostile	Frequently reacts aggressive and threatening toward humans.
Timid	Exhibits fear toward humans, retreats readily from humans, not tame.
Affiliative	Seeks companionship/company of humans, prefers not to be alone.

2.3.3. Data analysis

The methodology we used does not standardize behavioural observations (Carlstead 1999) and it is thus important to assess the repeatability and consistency of ratings between observers. We estimated the inter-observers reliability of the behavioural assessments on 2 levels: we measured the overall degree of agreement between observers for 12 animals and we measured the relative reliability of each behaviour item of the questionnaire.

Estimates of the relative reliability of each behaviour item are needed to determine which elements are the most consistent descriptions of the animal's character and which were the least and should be thus eliminated from the study (Carlstead 1999). For this, we calculated Kendall's coefficient of concordance (W) for each item. Items on which inter-observers reliability was below $W=0.5$, the point at which concordance coefficients failed to reach statistical significance at the level of $p<0.05$, were subsequently excluded from further analysis. Similarly, we tested the inter-observers reliability for an individual using Kendall's coefficient of concordance (W). Degree of association among the three raters was calculated on 12 wolves. If some animals had very low and non-significant coefficients ($W<0.5$, $p>0.05$), they were eliminated from the study.

Data were entered in a computerized database, with name, sex, age of separation from the pack (in weeks), origin, raising method, human contacts and human frequency for each animal. Inter-correlations between items were examined in a matrix. We used the single scores for 45 wolves that were rated by one observer and the average of the ratings on each item calculated over the three observers for the 12 remaining individuals. Those scores formed the input for a principal component analysis (PCA). PCA is a variable reduction procedure that explores redundancy in a set of variables. It linearly transforms the original set of variables into a smaller set of uncorrelated (orthogonal) components that capture most of the variation and information of the original set of variables. This technique has been used in previous studies for analyzing similar type of data collected in this study (Gold & Maple 1994, Gosling 1998, Carlstead 1999, Wielebnowski 1999, Wemelsfelder *et al*. 2000).

The relevant remaining components were then compared to the variables gender, origin, human contacts and human frequency using a Mann-Whitney U-test. We used Kruskal-Wallis test to compare the components to the variable raising method; and a Pearson correlation test to look for correlation of the components with the variable age of separation from the pack. Statistical significance was assumed at the level of $P<0.05$ for all tests. Statistical analysis, were carried on the software XLSTAT 2011.

2.4. Results

2.4.1. Inter-observers reliability

Table 2.3: Kendall coefficients of concordance (W) for three observers on 21 questionnaire items measured on 12 wolves.

Behaviour trait	Kendall inter-observers concordance coefficient
Active	0.528
Bold	0.784
Calm	0.573
Confident	0.528
Curious	0.514
Eccentric	0.560
Fearful	0.533
Greedy	**0.329**
Imaginative	0.602
Moody	**0.304**
Playful	0.535
Smart	**0.311**
Vigilant	**0.227**
Vocal	0.577
Aggressive	0.586
Friendly	0.551
Sociable	0.532
Warm	0.559
Hostile	**0.192**
Timid	0.751
Affiliative	0.861

For 16 of the 21 behavioural items, observer concordance coefficients ranged from W=0.51 to 0.86 (Table 2.3). Five items, greedy, moody, smart, vigilant and hostile, were excluded from further analysis as observer concordance coefficients ranged from W=0.19 to 0.33.

For 10 of the 12 wolves, observer concordance coefficients ranged from W=0.51 to 0.79 (Table 2.4). Two individuals, Martes and Shila, were excluded from further analysis as observer concordance coefficients W=0.32 to 0.33 respectively.

Table 2.4: Kendall coefficients of concordance (W) for three observers on 12 wolves rated on 21 questionnaire items.

Wolf individual	Kendall inter-observers concordance coefficient
Lunes	0.759
Martes	**0.329**
Miercoles	0.566
Sabado	0.587
Durimar	0.542
Philosph	0.793
Albert	0.558
Joerik	0.532
Shila	**0.332**
Cleopa	0.603
Steffi	0.509
Prossia	0.537

2.4.2. Relevant behavioural traits

PCA was performed with the scores of 55 wolves on 16 items and resulted in five components with eigenvalues >1, accounting for 79% of the observed variance (Table 2.5). We labelled these components according to the variables showing the highest positive loading: affiliative-bold (component 1), warm-friendly (component 2), eccentric-playful (component 3), confident-timid (component 4) and playful-aggressive (component 5).

Component 1 showed high positive loadings on the following variables: affiliative, bold, vocal and confident, and high negative loadings for timid and fearful. Component 2 had high positive loadings on the variables warm, friendly, sociable and playful, and high negative loading on aggressive. Component 3 showed high positive loadings for the variables rating eccentricity and playfulness, and high negative loadings for confidence and boldness. Component 4 had high positive loadings on the variables eccentric, confident and timid, and high negative loading on affiliative and vocal. Component 5 showed high positive loading for the variable rating playfulness and aggressiveness, and high negative loadings for active and affiliative (Table 2.5).

Table 2.5: Five major components of individual behavioural variation in wolves derived from score results of observer questionnaires on 55 wolves at the Biological Station "Chisty Les" obtained through principal component analysis.

	Components				
	F1	F2	F3	F4	F5
Active	0.379	-0.109	0.151	0.251	-0.410
Bold	**1.052**	-0.181	-0.454	0.288	-0.108
Calm	0.793	0.224	-0.361	-0.104	0.225
Confident	0.972	0.006	-0.519	**0.474**	0.115
Curious	0.532	0.132	-0.030	0.269	-0.089
Eccentric	0.283	-0.243	**0.632**	0.762	-0.196
Fearful	-0.951	-0.092	0.333	0.047	-0.044
Imaginative	0.223	0.182	0.056	0.421	-0.183
Playful	0.335	0.512	**0.470**	0.142	**0.550**
Vocal	1.039	-0.127	0.401	-0.256	0.162
Aggressive	0.623	-0.753	0.249	0.141	**0.509**
Friendly	-0.153	**0.606**	0.243	0.209	0.008
Sociable	0.065	0.585	0.164	0.106	0.126
Warm	0.028	**0.890**	-0.171	0.152	0.026
Timid	-1.118	-0.099	-0.197	**0.461**	0.117
Affiliative	**1.175**	0.227	0.369	-0.440	-0.396
	F1	F2	F3	F4	F5
Eigenvalues	8.381	2.622	1.877	1.803	1.100
Variance (%)	42.119	13.179	9.431	9.061	5.529
% cumulated	42.119	55.298	64.729	73.790	79.319

2.4.3. Impact of social and environmental criteria

We tested for differences in component scores of males/females, wild caught/captive-bred, daily/weekly human contact, contact with few/many people, and feeder/foster/tutor raising method. We also tested the correlation between component scores and age of separation from the pack (Table 2.6).

There was significant difference between males and females for components 2 and 3 (F2: $\bar{x}_{female} = 0.35$, $\bar{x}_{male} = -0.42$, $P<0.05$; F3: $\bar{x}_{female} = 0.32$, $\bar{x}_{male} = -0.38$, $P<0.05$). There was significant difference between wild caught and captive-bred for components 1 and 4 (F1: $\bar{x}_{hunter} = 1.13$, $\bar{x}_{zoo} = -1.46$, $P<0.05$; F4: $\bar{x}_{hunter} = -0.43$, $\bar{x}_{zoo} = 0.55$, $P<0.05$). There was significant difference between wolves with daily human contact and those with weekly human contact for components 3 and 4 (F3: $\bar{x}_{daily} = -0.29$, $\bar{x}_{weekly} = 0.52$, $P<0.05$; F4: $\bar{x}_{daily} = -0.59$, $\bar{x}_{weekly} = 1.04$, $P<0.001$). There was significant difference between wolves which had contact with few people and those which had contact with many people for component 4 ($\bar{x}_{few}$ = -0.17, $\bar{x}_{many}$ = 1.02, P<0.05). There was significant difference between wolves raised by feeder, foster or tutor method for components 1 and 4 (F1: $\bar{x}_{feeder}$ = -1.89, $\bar{x}_{foster}$ = 0.25, $\bar{x}_{tutor}$ = 2.08, P<0.01; F4: $\bar{x}_{feeder}$ = 0.60, $\bar{x}_{foster}$ = -0.05, $\bar{x}_{tutor}$ = -0.68, P<0.05). There was significant correlation with the age of separation from the pack for components 1, 3 and 5 (F1: r = -0.64, P<0.001; F3: r = -0.33, P<0.05; F5: r = -0.38, P<0.01) (Table 2.6).

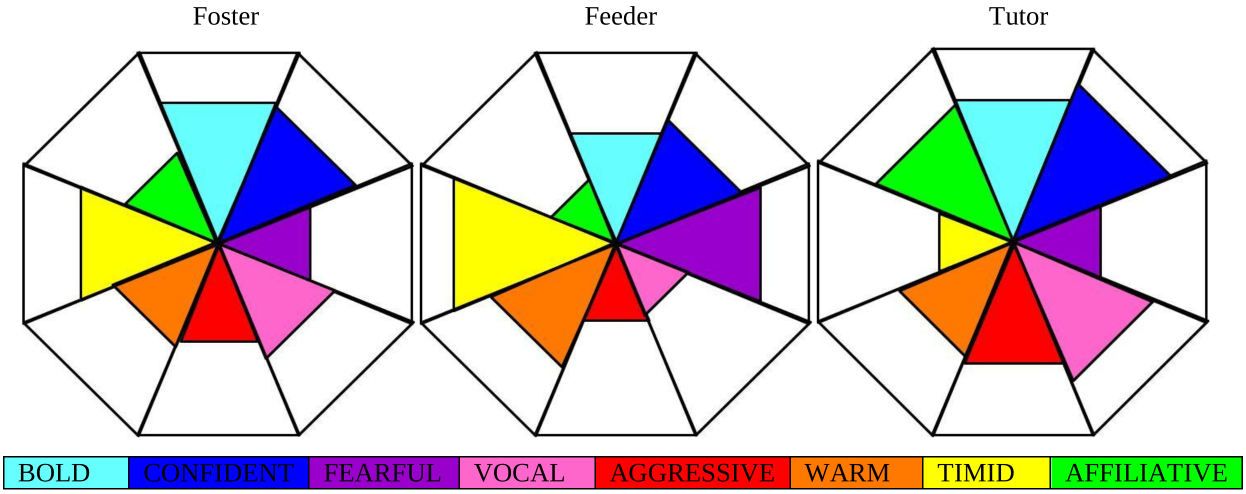
We drew behavioural profiles of wolves grouped by raising method using the mean scores in 8 behavioural traits: bold, confident, fearful, vocal, aggressive, warm, timid and affiliative (Fig.2.3).

Table 2.6: Mean and standard deviation of component scores of individual wolves grouped by gender, origin, human frequency, human contact, raising method, and age of separation from the pack.

	Components					
	Criteria	F1	F2	F3	F4	F5
Gender	Females (n=30)	x̄ = -0.06 ± 3.00	x̄ = 0.35 ± 1.82	x̄ = 0.32 ± 1.41	x̄ = -0.08 ± 1.51	x̄ = -0.17 ± 0.99
	Males (n=25)	x̄ = 0.07 ± 2.89	x̄ = -0.42 ± 1.29	x̄ = -0.38 ± 1.28	x̄ = -0.09 ± 1.16	x̄ = 0.20 ± 1.12
	Mann-Whitney test	U=374 P=0.99	U=243 P=0.03*	U=253 P=0.04*	U=413 P=0.53	U=448 P=0.22
Origin	Hunter (n=31)	x̄ = 1.13 ± 2.35	x̄ = -0.28 ± 1.65	x̄ = -0.01 ± 1.29	x̄ = -0.43 ± 1.10	x̄ = -0.06 ± 0.96
	Zoo (n=24)	x̄ = -1.46 ± 2.98	x̄ = 0.36 ± 1.57	x̄ = 0.01 ± 1.52	x̄ = 0.55 ± 1.47	x̄ = 0.08 ± 1.19
	Mann-Whitney test	U=547 P=0.00*	U=308 P=0.28	U=335 P=0.54	U=221 P=0.01*	U=345 P=0.65
Frequency	Daily (n=35)	x̄ = 0.50 ± 2.88	x̄ = 0.14 ± 1.55	x̄ = -0.29 ± 1.48	x̄ = -0.59 ± 1.03	x̄ = -0.00 ± 1.02
	Weekly (n=20)	x̄ = -0.86 ± 2.86	x̄ = -0.24 ± 1.79	x̄ = 0.52 ± 1.04	x̄ = 1.04 ± 1.24	x̄ = -0.00 ± 1.15
	Mann-Whitney test	U=437 P=0.13	U=398 P=0.41	U=218 P=0.02*	U=112 P<0.001***	U=358 P=0.90
Contact	Few (n=47)	x̄ = -0.09 ± 3.02	x̄ = 0.15 ± 1.49	x̄ = 0.02 ± 1.43	x̄ = -0.17 ± 1.28	x̄ = 0.02 ± 1.03
	Many (n=8)	x̄ = 0.51 ± 2.37	x̄ = -0.87 ± 2.34	x̄ = -0.12 ± 1.12	x̄ = 1.02 ± 1.44	x̄ = -0.10 ± 1.31
	Mann-Whitney test	U=174 P=0.75	U=249 P=0.15	U=200 P=0.78	U=101 P=0.04*	U=211 P=0.59
Method	Feeder (n=21)	x̄ = -1.89 ± 2.93	x̄ = 0.29 ± 1.94	x̄ = -0.15 ± 1.65	x̄ = 0.60 ± 1.45	x̄ = -0.12 ± 1.22
	Foster (n=17)	x̄ = 0.25 ± 1.94	x̄ = -0.39 ± 1.19	x̄ = -0.24 ± 0.91	x̄ = -0.05 ± 1.26	x̄ = 0.10 ± 0.78
	Tutor (n=17)	x̄ = 2.08 ± 2.23	x̄ = 0.03 ± 1.63	x̄ = 0.43 ± 1.39	x̄ = -0.68 ± 1.00	x̄ = 0.05 ± 1.14
	Kruskal-Wallis test	K=16.67 P=0.00**	K=2.54 P=0.28	K=0.97 P=0.62	K=8.65 P=0.01*	K=0.58 P=0.75
Age	Pearson correlation test	r = -0.638 P<0.001***	r = -0.095 P=0.49	r = -0.325 P=0.02*	r = 0.051 P=0.71	r = -0.379 P=0.00**

Significance levels: *P<0.05; **P<0.01; *** P<0.001

Fig 2.3: Behavioural profiles of wolves grouped by raising method.



2.5. Discussion

2.5.1. Influence of environment on behaviour

By analyzing the influence of various criteria on wolves' scores, we tried to identify those which may later impact on performance (Fig 2.4). As expected, early raising experiences, especially with regard to social and environmental conditions, seem to play an important role in shaping an individual's tendencies to be confident. The origin of the wolves, the frequency and number of human contacts they had, and the raising method have influence on their level of confidence (component 4). Origin, raising method, and age of separation from the pack have also an impact on wolf level of boldness (component 1). Impact of raising conditions on behaviour was demonstrated for other species, such as chimpanzees (Walsh *et al*. 1982), dogs (Fox & Stelzner 1966), domestic cats (Guyot *et al*. 1980), silver foxes (*Vulpes vulpes*) (Pederson 1993), or rabbits (*Oryctolagus cuniculus*) (Kerstner *et al*. 1989). Carlstead & Shepherdson (1994) suggested that animals raised in a socially deficient environment may be less able to cope with novel and stressful situations. The wolves taken from zoo stayed longer in familiar and secure environment than the pups caught by hunter. Although pups are captive in zoo, they are well-fed, protected and surrounded by the pack. Caught by hunters, pups experienced the stress of caught, remove from the family and usually bad handling and caging for a while. Fox (1972) demonstrated that fearless wolf pups were more exploratory, and had less hesitation to kill in a prey-situation. With dog pups, although Wright (1983) did not find difference in exploratory behaviour due to raising method, he showed that stimulus reactivity was significantly affected by raising method at 8.5 weeks with hand-reared pups investigating and spending more time in the presence of the novel objects than mother-reared. Wielebnowski (1999) found lower scores of fearfulness and aggressiveness for hand-reared cheetahs than mother-reared, but Mellen (1992) found human-reared domestic cats more aggressive than mother-reared. From our experience, wolf pups taken later from the pack were less aggressive with conspecifics, possibly because the longer the pups stay with the pack, the higher chance that the parents already stopped violent fights between the pups and showed the ritualised rules of the pack. Sociability and playfulness seem to have similar scores, and environment or social criteria have little impact on these items. Levels for affiliative vs. timid were mostly influenced by origin of pups and raising method used, with wolves from zoo more timid towards human than wolves from hunters, and pups raised with foster wolves more timid than human-raised pups. When we get the pups at 2 weeks old, usually from hunter, they often display tameness towards human, and we expect to change this tendency by placing them with adult wolves, with more or less success. When pups are separated from the pack between 3 and 5 weeks, either from hunters or zoos, they display very various behaviours towards human, from tame to fearful. On those pups, the foster raising method had shown very good results in reversing the tameness tendency. Taken after 6 weeks old from zoo, wolf pups usually display high level of fearfulness towards human. Although sample sizes are too small to make any conclusion, it is interesting to note that among the pups of 2 weeks old, the foster raising method tends increase the level of timidity and decrease the one of affiliativeness. This tendency is less significant among the pups of 3-5 weeks, with whom both foster and feeder raising methods tend to increase the level of timidity and decrease the one of affiliativeness (Fig 2.5).

Fig 2.4: Influence of environment on individual behaviour and on animal performance (adapted from Carlstead 1999).

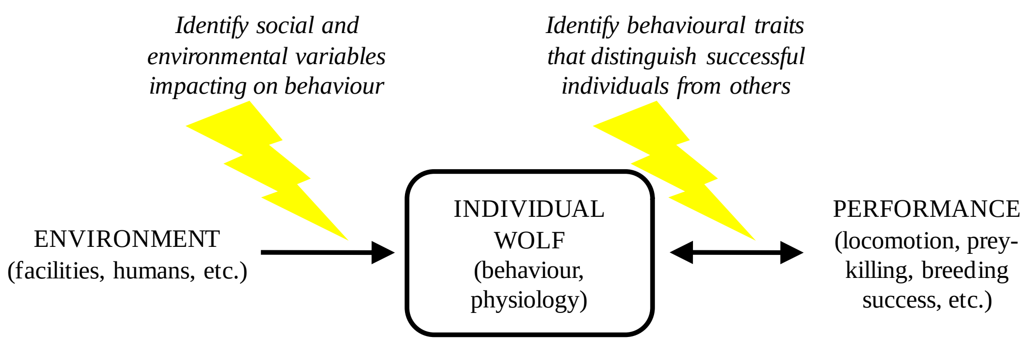
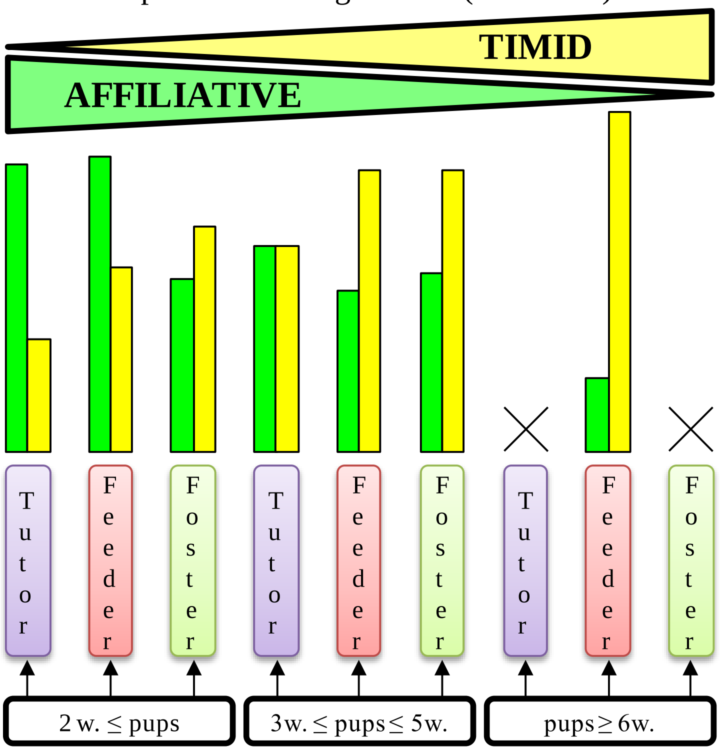


Fig 2.5: Average scores of timidity and affiliativeness depending on age of separation from the pack and raising method (w.=weeks).



2.5.2. Inter-species personality comparison

Although species are very different from each other, we found interesting to make a cross-species comparison of the personality components found in previous studies on various mammals (Table 2.7). The components found for wolves in this study appear to be equivalent to personality dimensions reporter for other species. Especially boldness, sociability (warm-friendly), playfulness and aggressiveness are found in many other species. Less surprising, the main components found in our study are very close to those found with dogs (Svartberg & Forkman 2002).

Table 2.7: Cross-species literature review of main components found in animal personality.

Species	Components	Reference
Grey wolf (*Canis lupus*)	*affiliative-bold* *warm-friendly* *eccentric-playful* *confident-timid* *playful-aggressive*	*Present study*
Dog (*Canis familiaris*)	playfulness curiosity/fearlessness chase-proneness sociability aggressiveness	Svartberg & Forkman 2002

Spotted hyena (*Crocuta crocuta*)	assertiveness excitability human-directed agreeableness sociability curiosity	Gosling 1998
Cats (*Felis catus*)	shy trustful	Meier & Turner 1985
Cheetah (*Acinonyx jubatus*)	tense-fearful vocal-excited aggressive	Wielebnowski 1999
Pig (*Sus domesticus*)	aggression sociability exploration	Forkman *et al*. 1995
Vervet monkey (*Cercopithecus aethiops*)	socially competent playful/curious opportunistic	McGuire *et al*. 1994
Rhesus monkey (*Macaca mulatta*)	affiliative hostile fearful	Chamove *et al*. 1972
Rhesus monkey (*Macaca mulatta*)	confidence excitability sociability	Stevenson-Hinde & Zunz 1978
Rhesus monkey (*Macaca mulatta*)	confident-popular/tense-insecure motherly-eccentric/playful-active aggessive-irritable solitary	Bolig *et al*. 1992
Chimpanzee (*Pan troglodytes*)	dominance sociability machiavellianism anxiety	Dutton *et al*. 1997
Gorilla (*Gorilla gorilla*)	extroverted dominant fearful understanding	Gold & Maple 1994
Human	extraversion neuroticism psychoticism	Eysenck & Eysenck 1969

These components may also be comparable to the major factors used to describe human personality, in particular the three-factor structure identified by Eysenck & Eysenck (1969): extraversion, characterized by sociable behaviour; neuroticism, characterized by anxious behaviour; and psychoticism, characterized by hostile, aggressive, or dominant behaviour.

From this overview, it seems that the trait reflecting sociability is shared in most species, obviously due to the comparable demands of group living (Dutton *et al*. 1997). Calculating correlations between 4 studies (Stevenson-Hinde & Zunz 1978, Bolig *et al*. 1992, Gold & Maple 1994, Gosling 1998), Gosling (1998) found that assertiveness-dominance was the major component, together with the elements excitability and sociability.

The wolf females in our study were less bold and confident and more fearful and timid than males, although difference was not significant. Sexual difference in fear behaviour has been reported for various species in previous studies. Females of dogs (Goddard & Beilharz 1983), chimpanzees (Buirski *et al*. 1978) and cheetahs (Wielebnowski 1999) were found more fearful than males. Buirski *et al*. (1978) suggested that the need for females to protect offspring and be more watchful could explain the difference.

Gosling (1998) found a factor untitled human-directed agreeableness with spotted hyenas which did not correlate with primate research. He made the hypothesis that this factor could be relevant to captive animals, where humans are a major part of the social environment. Our findings of the importance of the component affiliative-bold, explaining 42% of the variance, go in the same sense. Social carnivores are well-known for their ability to form relationships with humans (Fentress 1992) and this component may reflect this sensitivity.

Our study revealed the importance of the bold-shy continuum, as previous studies on various species did (Wilson *et al*. 1994). This fundamental behavioural trait reflecting individual's level of boldness, anxiety or calmness, and degree to which it will take risks or explore new environments may have important consequences on animal performance. Bremner-Harrison *et al*. (2004) already demonstrated that bolder reintroduced swift foxes had higher mortality risk after release. Here, bolder wolves were also the more affiliative towards people, which likely induce a higher risk of exposure to human mortality (hunting, traffic, etc.). On the other side, confidence and fearlessness, partly represented in bold behaviour, have been shown to play important role in prey-killing success (Fox 1972). Therefore the level of boldness should be at an optimum to cope with both predator avoidance and prey-killing.

2.5.3. Reliability of the method

Once removed the items or individuals with low inter-raters concordance, we found average 0.6 of concordance on ratings between observers among behavioural items and among wolves. Although many studies, on a large range of species (e.g., rhesus monkeys, (Stevenson-Hinde & Zunz 1978, Bolig *et al*. 1992), spotted hyenas (Gosling 1998), domestic cats (Feaver *et al*., 1986), and cheetahs (Wielebnowski 1999)), attested the validity of observer ratings, one may wonder the scientific value of subjective assessments of animal behaviour. In most of those studies, raters had more than 200 hours of observation with the animals before assessment. Martau *et al*. (1985) also highlighted the importance of familiarity in reliable assessments. Truly, people caring for animals and spending many hours watching them, often feel that individuals have distinct personalities (Feaver *et al*. 1986). And it is worth noting that judgments of behaviour in animals are not based upon verbal reports of subjective states, but are inferences made by human observers on the basis of various evidences including behavioral interactions, displays, prior events, subsequent outcomes, and the behavior of other animals towards the subject observed (Buirski & Plutchik 1991). However, some researchers have noticed a low inter-raters reliability in particular situations: for subjects whose social status was undergoing change and for young individuals (Martau *et al*. 1985). It was also reported that some ratings may have been influence by the expectations and assumptions of the raters (for example ‘males are more aggressive than females’) (Dutton *et al*. 1997). But those cases were found only with primate species and we expected less mirror interpretation with species far from human taxa such as wolves.

However, while qualitative assessments of behaviour of other humans have become widely accepted in psychiatric research (Carlstead 1999), the method is still criticized for its subjective interpretation of observations in animal research (Réale *et al*. 2007). That is why, for logistical and methodological reasons, Réale *et al*. (2007) advised to measure temperament traits in experimental contexts, but admitted this option is also open to criticism as it places the animal in a situation irrelevant to its natural conditions. Moreover, Wemelsfelder *et al*. (2000), insist on the irrelevant argument of objectivity, as long as human beings, including scientists, are part reality and act upon it. Thus, qualitative behavioural measurement does not differ fundamentally from standard physiological and behavioural measurement in its dependence on human perception (Wemelsfelder *et al*. 2000).

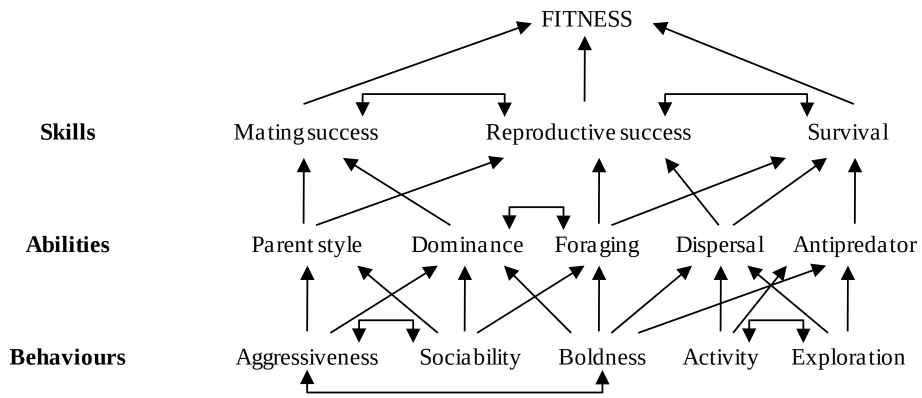
Therefore, for future research on animal personality, Gosling (1998) suggests (1) to ensure that the behavioural traits adequately represent the full range of individual differences in the behaviour of the target species, (2) to use similar items and rating scales across studies to facilitate comparison, (3) to clearly define the sample population, (4) to allow replication of the study, and (5) to compare ratings to monitored tests when possible. In conclusion human observers and their perceptive powers can be reliably used as an assessment tool to increase our knowledge on animal behaviour (Wemelsfelder *et al*. 2000).

2.5.4. Recommendations for reintroduction programmes

In general consideration of captive animals, such research allows better understanding of biological and environmental influences on personality and our increasing knowledge of animal behaviour can serve animal welfare. Buirski & Plutchik (1991) suggested testing captive animals and comparing them to free-living animals to understand to which extent their psychological state is affected by captivity. In some cases, environmental enrichment will reduce captive stress and improve animal welfare. Our knowledge about temperament will also help optimizing captive reproduction and increasing reintroduction success (Wilson *et al*. 1994).

For this purpose, we suggest to first identify the main important behavioural traits involved in foraging, breeding, defensive and locomotory skills (Fig 2.6). This can be done by comparing behaviours of wild-caught vs. captive-bred individuals, on personality dimensions and in tests evaluating anti-predator, exploratory, hunting and mating performance. When the characteristics that appear deficient in captive-bred animals are identified, it would be necessary to identify the environmental and social criteria (facilities, humans, etc.) at their origin and to evaluate the impact of interventions such as enrichment. Secondly, a simple and quick test should be drawn up to select the candidates for reintroduction. It could be mostly done on behavioural assessments by direct observation as long as the method has been proved reliable, does not require animal handling and can be done by animal keepers.

Fig 2.6: Relations between behavioural traits, animal abilities and appropriate skills (adapted from Réale *et al*. 2007).



Research has showed more and more evidence that captivity influences animals' abilities to survive and results in animals lacking 'wild' type behaviours (Rabin 2003). The review of Jule *et al*. (2008) reported that behaviours associated with tameness towards humans, lack of social influence from conspecifics, and lack of foraging/hunting skills are factors that should be investigated more thoroughly in order to improve upon the survival of captive-born released carnivores. More research is particularly needed to understand the effects of husbandry and pre-release experience of the survival of released animals (Jule *et al*. 2008). Previous studies (McPhee 2003, Mathews *et al*. 2005, Jule *et al*. 2008) suggested to systematically compare captive-bred individuals to wild animals before reintroduction.

However, this seems to be soon constrained by practical limits, especially with large mammals. McPhee (2003) and Mathews *et al*. (2005) worked with old-field mice (*Peromyscus polionotus*) and bank voles (*Clethrionomys glareolus*) as models respectively, which are small-sized, can be studied on large samples and several generations, and are not endangered. The issue would be much less easy with reintroduction of black rhinoceros (*Diceros bicornis*), for example. In this view, our present study on behavioural traits of wolves both from captive-bred and wild-caught stocks may be useful for canids reintroduction programmes in general. Although we did not test wolves in practical situations relevant to their reintroduction, we did not find much difference in behaviour of captive-bred vs. wild-caught, except for their behaviour towards human. Tendency runs counter general belief that captive animals display less fear towards human than in the wild. The study shows that more important than captivity/freedom is the factor of time spent within the pack, especially when dealing with young animals. Pazhetnov & Pazhetnov (2005) experienced similar results with captive-born bear cubs. Taken at about 3 months old from the bear female in zoo, there were no difficulties in releasing these animals into the wild as they developed a strong avoidance of humans.

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Chapter 3. Early post-release movements of reintroduced wolves in Russia

Chapitre 3. Premiers mouvements post-relâché de loups réintroduits en Russie

Глава 3. Первые перемещения после выпуска волков в России

3.1. Abstract

Abstract: The biology of reintroduction is still at its infancy and needs serious rigorous success evaluation, especially during post-release monitoring. Captive animals released frequently displayed erratic movement behaviour and are exposed to high risk of mortality. Since 1993, hand-reared wolves have been released into the wild, at the Biological Station Chisty Les (Toropetsky raion, Tverskaya oblast, Russian Federation). For the first time in 2010, 6 wolves were equipped with GPS/Argos collar of brand ES-PAS. Coordinates were received by daily connection to the Argos server, then checked in the field when possible. All points were geographically placed thanks to the cartography program OziExplorer. This study shows the first results after 6 month-long monitoring. The collared worked from 1 day to 6 months, and gave about 450 locations. The results show interesting differences in the territory-use of wolves and in their movements of dispersion, that we compared with the dispersal behaviour of wild wolves. The roles of individual behaviour and type of release (hard/soft) are also discussed to explain those differences. We gave some results on the performance of those first GPS collars deployed on wolves in Russia, and recommendations to future release of captive-raised animals.

Key words: *Canis lupus*, GPS-Argos, monitoring, dispersion, reintroduction.

Résumé : La biologie de la réintroduction en est encore à ses débuts et a besoin de sérieuses et rigoureuses évaluations du succès, en particulier lors des suivis post-relâché. Les animaux captifs relâchés présentent souvent un comportement de déplacement erratique et sont exposés à un fort degré de mortalité. Depuis 1993, des loups élevés en captivité sont relâchés dans la nature, à la Station Biologique Chisty Les (Toropetsky raion, Tverskaya oblast, Fédération de Russie). Pour la première fois en 2010, 6 loups ont été équipés de collier de type GPS/Argos du constructeur ES-PAS. Les coordonnées étaient reçues par connexion quotidienne au serveur Argos, puis examinées sur place. L'ensemble des points a été placé géographiquement grâce au logiciel de cartographie OziExplorer. Cette étude présente les premiers résultats après 6 mois de suivi. Les colliers ont fonctionné de 1 jour à 6 mois et donné plus de 450 localisations. Les résultats montrent des différences intéressantes dans l'utilisation du territoire des loups, et dans leurs mouvements de dispersion, que nous comparons avec le comportement de dispersion des loups sauvages. Les rôles du comportement individuel et du type de relâché (hard/soft) sont également discutés pour expliquer ces différences. Nous donnons aussi des résultats sur la performance de ces premiers colliers GPS déployés sur des loups en Russie, ainsi que des recommandations pour les relâchés futurs d'animaux élevés en captivité.

Mots-clés : *Canis lupus*, GPS-Argos, suivi, dispersion, réintroduction.

Абстракт: Биология реинтродукции лишь развивается и нуждается в серьезных и точных оценках успеха, в особенности в течение слежения после выпуска. Выращенные в неволе и затем выпущенные животные часто показывали поведение блуждающих перемещений и подвергались высокому риску смертности. Начиная с 1993 г. выпускали выращенных в неволе волков на Биологической Станции «Чистый Лес» (Торопецкий район, Тверская область, Российская Федерация). Впервые в 2010 г, 6 волков были оснащены GPS/Argos ошейником фирма ЕС-ПАС. Координаты были получены ежедневно по связи с сервером Аргоса, затем рассмотрены на месте когда это было возможно. Все точки были географически помещены на карту по программе картографии OziExplorer. Это исследование представляет первые результаты после 6 месяцев слежения. Ошейники работали от 1 дня до 6 месяцев и дали более 450 локализаций. Результаты показывают интересные различия в использовании территории волками и в их расселении, которые мы сравниваем с поведением диких волков. Роли индивидуального поведения и типа выпуска (hard/soft) также обсуждены, чтобы объяснить те различия. Мы даем некоторые результаты использования этих GPS

ошейников одетых на волков в России, и рекомендации для будущих выпусков животных в неволю.

Ключевые слова: *Canis lupus,* GPS/Argos, слежение, расселение, реинтродукция.

3.2. Introduction

The biology of reintroduction is still at its infancy (Seddon *et al*. 2007, Armstrong & Seddon 2008, Gusset 2009). Many attempts of reintroduction were mainly based on subjective beliefs and the absence of rigorous evaluation seems to be an obstacle in promoting conservation biology as a scientific discipline (Kleiman *et al*. 2000, Stem *et al.* 2005). Reintroduction programs have an urgent need of scientific evidence (Sutherland *et al.* 2004), especially during pre and post-release monitoring (Hunter 1998).

The release of an animal into an unknown territory, whether it involves the translocation of wild animals, reintroduction of captive-raised animals, or the rehabilitation of orphaned or sick animals, often produces unnatural behaviour and erratic movements (Bright & Morris 1994, Robertson & Harris 1995). Animal released and dispersing wild animals display periods of high movement activity, generally associated with high mortality (Robertson & Harris 1995). Site acclimation before release may be beneficial in reducing the risk of abnormal behaviour and mortality (Moore & Smith 1991).

The idea in such study is to understand if captive-raised wolves have “normal wild behaviour”. Dispersal is the process by which an animal searches for a new home range in which to settle, and captive-raised animals have to achieve the same goal in the period following their release (Robertson & Harris 1995). Wolves were released at 1-3 years old, in spring and summer, whereas wild wolves leave the family usually aged of 11-24 months (Fritts & Mech 1981, Peterson *et al*. 1984, Potvin 1988, Gese & Mech 1991, Hayes & Harestad 2000) from spring to autumn, with a peak at denning period (Gese & Mech 1991, Mech & Boitani 2003). In general, the dispersion is made in several round trips of the leaving members, temporary staying or leaving their pack, up to 6 times until they definitively leave it (Fritts & Mech 1981, Van Ballenberghe 1983, Peterson *et al*. 1984, Messier 1985, Potvin 1988, Fuller 1989, Gese & Mech 1991). The temporary trips could be seen as exploratory or in a need of feeding, or for social circumstances (Mech & Boitani 2003). Previous studies of the behaviour of dispersing red foxes (Storm & Montgomery 1975, Zimen 1984, Woollard &

Harris 1990, Robertson 1994) support the exploratory hypothesis and describe the dispersal in phases. The first two studies described rapid movements interspersed by periods spent on a temporary range, and movements following consistent compass bearing. The other two studies reported a series of exploratory trips from the natal range prior to the actual dispersal movement in a single night.

It seems to be no difference between sexes in distance covered, but some studies show that males dispersed farther, (Pulliainen 1965, Peterson *et al*. 1984, Wabakken *et al*. 2001), while other studies in other regions and other periods reported that females covered in average longer distance than males (Fritts 1983, Ballard *et al*. 1987).

Distances travelled are very various and reflect simple short movement to neighboured territory, up to long and complex travel, with animals crossing highways, open areas, passing big lakes or cities (Mech *et al*. 1995, Merril & Mech 2000, Wabakken *et al*. 2001). The maximum distance recorded worldwide is 1092 km (Wabakken *et al*. 2007). Data suggest that the younger the wolf, the farther it will move. This could be due to increasing social relationship within the pack for wolves that stay longer. Also maybe older wolves perceive better the local opportunities whereas naïve younger individuals would search for security farther and farther (Mech & Boitani 2003).

Data about direction of dispersion are few and should be used carefully. In a total homogenous habitat, wolves should disperse in all directions. But habitat is rarely homogenous and direction may be influenced by topography, wolf density, human exploitation (Mech & Boitani). A study of Boyd *et al*. (1995) reported that most of dispersing wolves in Montana (USA) settled north-west, where other wolves were already present. So it seems that the dispersion of wolves tends to optimize the chance of reproduction (search for partner) rather than the feeding resources (search for prey). Another study in Wisconsin (Wydeven *et al*. 1995) concluded in the same tendencies.

The aim of this study was to give the early results of post-release movements of first equipped captive-raised wolves released in Russia. We expected that wolves would undergo brief dispersal-type movements before settling on a temporary or permanent home place. We also made the hypothesis is that site acclimation is beneficial in reducing erratic movements. Finally the study should give some information on the performance of the first GPS/Argos collars deployed on wolves in Russia.

3.3. Material and methods

3.3.1. Individuals studied

Six wolves (Table 3.1), 2 males and 4 females, born in captivity (Belgorod zoo, Nijni-Novgorod zoo) or in the wild (Pskov region, Smolensk region) were raised at the Biological Station “Chisty Les” (Toropetsky raion, Tverskaya oblast), using different methods:

-Gay, Rem, Tassia (enclosure Puplovo): Feeder method: he/she feeds the pups without direct contact.

-Cleopa, Prossia, Steffi (enclosure Seriozha): Foster method: the pups are introduced to an adult female who behaves like their mother.

Table 3.1: Identity card of the 6 wolves equipped in the study.

Individual	GAY	REM	TASSIA	CLEOPA	STEFFI	PROSSIA
Photo						
Sex	M	M	F	F	F	F
Birth	2007	2007	2007	2009	2009	2009
Origin	Nijni-Novgorod zoo	Nijni-Novgorod zoo	Belgorod zoo	Smolensk forest	Pskov forest	Pskov forest
Release site	Kaluzhsky Zaseki Zapovednik	Kaluzhsky Zaseki Zapovednik	Kaluzhsky Zaseki Zapovednik	Biological Station Chisty Les	Biological Station Chisty Les	Biological Station Chisty Les
Release date	23.03.2010	23.03.2010	23.03.2010	07.05.2010	18.06.2010	15.07.2010
ID collar	53266	53264	53265	55107	61704	98731

The wolves were kept in enclosures of 0.7 (enclosure Seriozha) to 1.5 ha (enclosure Puplovo) for several months. They were provided with food 2-3 times per week, with average amount of 1kg/wolf/day. The food provided is mainly meat from the slaughterhouse (chicken, pork, beef and horse), road kills (hare, birds), remains of hunting (wild boar, moose) or fish (whiting, cod, pout). No live prey was provided during the raising. However, in the enclosure, the wolves may catch small prey (insects, frogs, birds, rodents) and eat vegetation available (grass, berries).

After release, supplemental food (carcasses mainly composed of bones and little meat) was regularly provided temporarily at enclosure Seriozha as a support for the newly released wolves.

3.3.2. Study area

The Biological Station “Chisty Les” (56°44’N, 31°31’E) is situated 450 km north-west from Moscow, in the district of Toropets (3373 km^2), in the region of Tver, in Russian Federation. Spruce *(Picea abies)* and pine *(Pinus sylvestris)*, together with birch *(Betula pendula)*, aspen *(Populus tremula)*, and alder *(Alnus incana)* dominate the terrain. The human density is about 6.5 inhabitants/km^2. The climate is continental with two main seasons, winter and summer. Averages temperatures vary between -17°C in January and +17°C in July. Annual precipitations are 550-750 mm. The slightly hilly terrain, called the Valday highlands, has elevations ranging from 220-270 meters above sea level. Poorly drained clays are widespread in the area and give rise to swamps, bogs and peats.

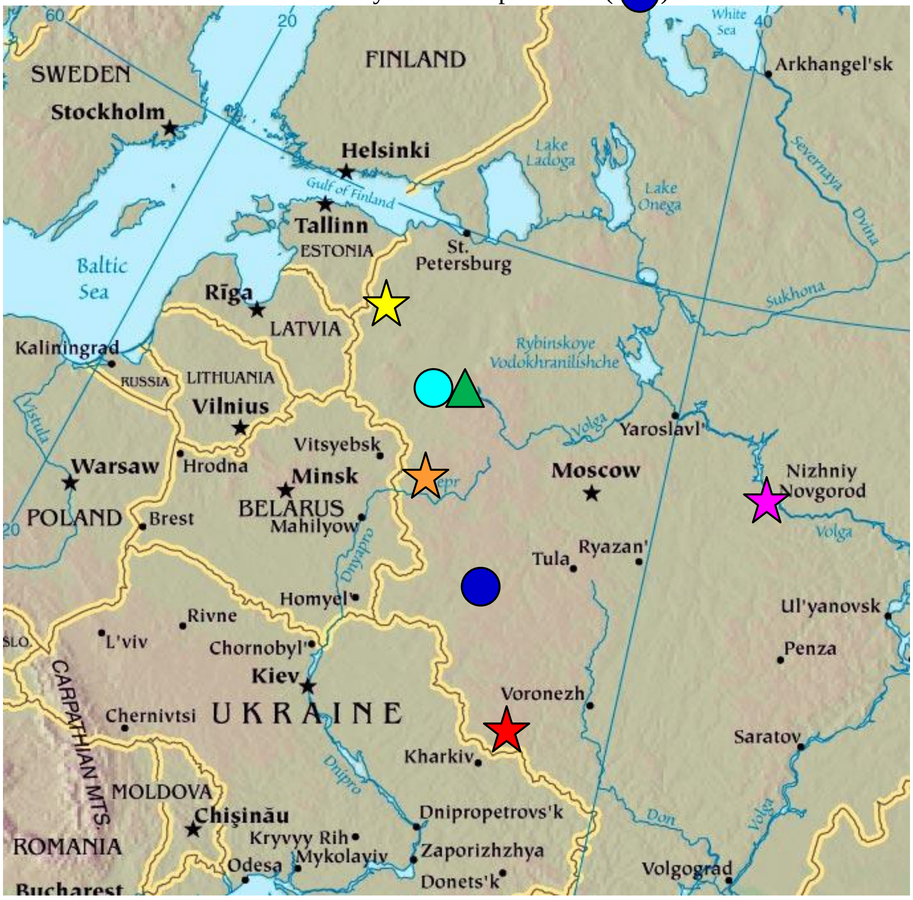
The Kaluzhsky Zaseki Zapovednik (53°43’N, 35°32’E) is situate 250 km south-west from Moscow, in the district of Ulyanov (1656 km^2), in the region Kaluga, in Russian Federation. Pedunculate oaks (*Quercus robur*), Scotch elms (*Ulmus scabra*), small-leaved lime (*Tilia cordata*), common ash (*Fraxinus excelsior*), together with Norway and common maple (*Acer platanoides, A. campestre*) cover the terrain. The human density is about 4.5 inhabitants/km^2. The climate is continental with two main seasons, winter and summer. Averages temperatures vary between -9°C in January and +18°C in July. Annual precipitations are 700-830 mm. The landscape is flat with characteristic moraines and gentle hills.

3.3.3. Animal equipment and release

Between March and July 2010, then aged of 1 to 3 years old, these wolves were released at the Biological Station itself or at the Kaluzhsky Zaseki Zapovednik (Fig 3.1). So as to follow the released wolves, each of them was equipped with a GPS/Argos collar of brand ES-PAS (Moscow, Russian Federation) (Fig 3.2).

Fig 3.2: GPS/Argos collar of brand ES-PAS (Moscow, Russian Federation).
Size: 205x50 mm (HxL), neck size: 37-42cm, weight: 500g.

Fig 3.1: Situation of the sites of origin, raising and release of wolves in Russian Federation: 2 males and 4 females, captive-bred (Belgorod , Nijni-Novgorod) or wild-caught (Pskov , Smolensk), were raised at the Biological Station "Chisty Les" ( ) and released at the Station ( ) or at the Kaluzhsky Zaseki Zapovednik ( ).



The Argos system of location and data collection uses a plat-form transmitter terminal (PTT) attached to the wolf via a collar. The ultra high frequency signal (401.650 MHz) emitted by the PTT is send to a satellite that relays the information to a terrestrial reception station. The station automatically transmits the data to a treatment centre, situated in Toulouse (France) (Collecte Localisation Satellite 2008). Numerous satellites go over a specific platform at approximately the same time every day (Fig 3.3). The user receives the data directly on its computer via Internet, after connection to ArgosServer.cls.fr thanks to the software Telnet (Fig 3.4). With the present collars, the Argos system was combined with a GPS device. The GPS receiver determines the new position with regular intervals and high precision. The location is sent at the time of the emission by the Argos beacon (every one or three emissions depending on the collar programmation). The collar weighs 650 g and had an operational life of about one year, with a schedule of 15 days in permanent working, then 4 h ON / 4 h OFF.

Wolves were immobilized with an intramuscular injection of Zoletil and Domitor at a dosage of approximately 3mg/kg and 30µg/kg of estimated body mass, respectively. Anaesthesia was necessary for the comfort in manipulation, the security of handlers and to reduce the stress of animals. Wolves were measured and weighed (Table 3.2), treated against endo and ecto-parasites (Dectomax 0.5ml/20kg, hypodermic injection), and fitted with GPS/Argos collar (Table 3.3).

Gay, Rem and Tassia were caged after immobilization in 120x80x50cm cages and transported by car to Kaluzhsky Zaseki Zapovednik (700km, 10h transport). On March, 23rd 2010, the wolves were released simultaneously at 13:15 (Fig 3.5) in the zapovednik, location (53°32’15”N, 35°40’00”E). They were thus “hard” released: released without a period of acclimation and without any subsequent provision of familiar food and shelter (Griffith *et al.* 1989).

Fig 3.3: Prediction of satellite passes over the Biological Station (56°43’53”N, 31°31’24”E), for the study period (source: ArgosServer.cls.fr).

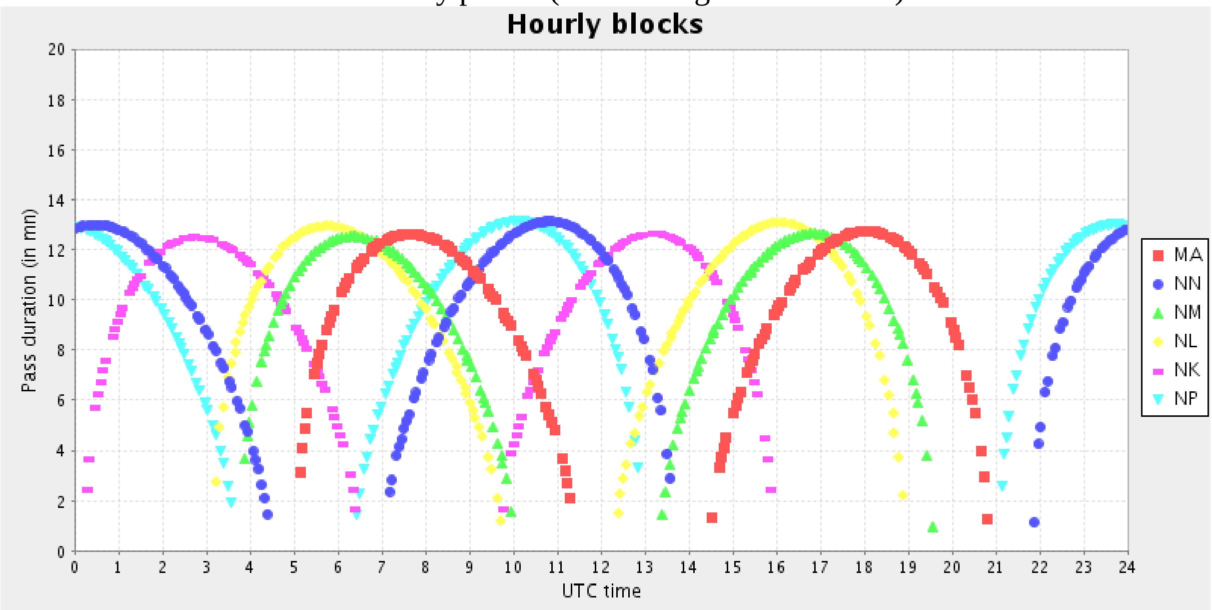


Fig 3.4: Functional process of the GPS/Argos collar, from the wolf to the researchers.

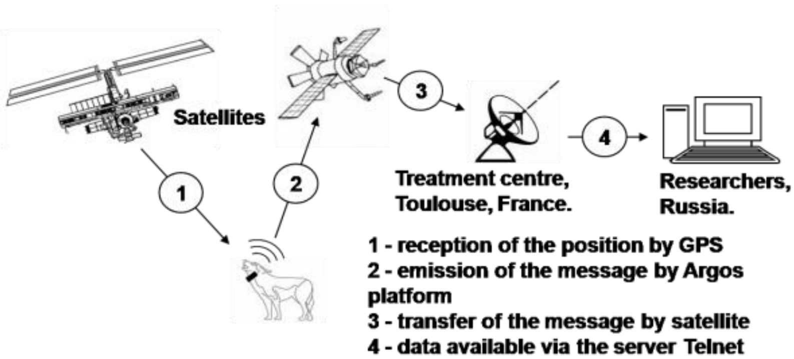


Fig 3.5: Release of Gay at the Kaluzhsky Zaseki Zapovednik on March, 23rd, 2010 (photo: V. Bologov).

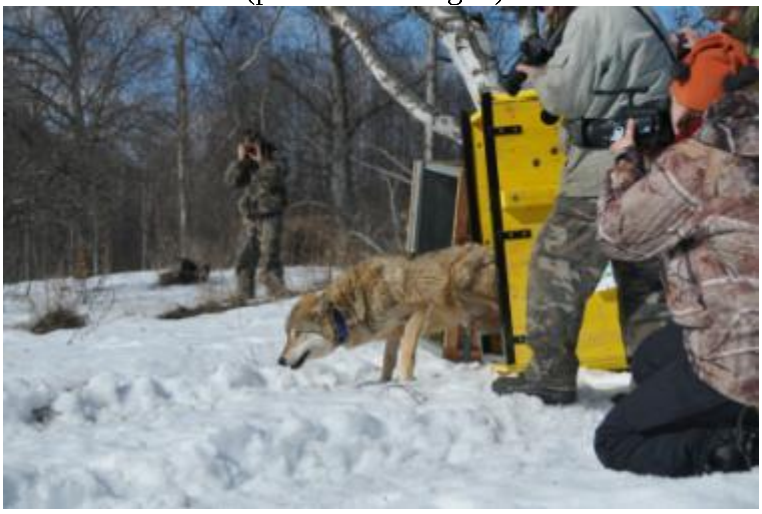


Table 3.2: Measures of the released wolves
(n/a: not available. Body length: from the neck to the bottom of the back).

Individual	GAY	REM	TASSIA	CLEOPA	STEFFI	PROSSIA
Weight (kg)	n/a	n/a	n/a	25	33	35
Body height (cm)	n/a	n/a	n/a	60	63	68
Head length (cm)	28	n/a	n/a	24	25	25
Body length (cm)	87	n/a	n/a	76	82	84
Tail length (cm)	35	n/a	n/a	28	30	35
Chest measurement (cm)	70	n/a	n/a	62	68	68
Collar size (cm)	n/a	n/a	n/a	37	40	42
Paw, LxW (cm)	n/a	n/a	n/a	8x6	8x5.5	8x6

Table 3.3: Programming characteristics of the 6 GPS/Argos collars deployed on wolves.

Collar ID	Period of emission of Argos messages	Period of definition of GPS coordinates
53264	65 secondes +/-10%	195 secondes +/-10%
53265	70 secondes +/-10%	600 secondes +/-10%
53266	120 seconds +/-10%	120 seconds +/-10%
55107	120 seconds +/-10%	120 seconds +/-10%
61704	70 seconds +/-10%	210 seconds +/-10%
98731	65 seconds +/-10%	130 seconds +/-10%

Cleopa, Prossia and Steffi were moved to neighbouring-fenced enclosure for the awakening, at enclosure Seriozha (56°44’45”N, 31°27’28”E), Biological Station “Chisty Les”. The day after anaesthesia, the enclosure was opened and the wolves went out when they wanted. They were thus “soft” released: released with a period of acclimation and with the provision of familiar food and shelter after release (Griffith *et al.* 1989).

3.3.4. Data collection and analysis

We collected the position of wolves by daily connection to Internet. All the points were geographically placed on map thanks to the map software OziExplorer. We examined the ultimate travel direction and ultimate distance moved from release site. Ultimate direction was the compass bearing from the release site to the site of mortality or last known location. Ultimate distance was the straight-line distance between those points (Fritts *et al*. 1994).

We classified the times of positions received by hour class (class 0 goes from 00:00:00 to 00:59:59), for each wolf and together. We examined the statistical data given by Telnet: number of all points, number of errors (non correct), number of errors (BCH correct).

Statistical analysis was performed with the software XLSTAT 2011.

3.4. Results

3.4.1. General results

Over the six collars fitted on released wolves, one never worked (ID 53264), possibly because the battery empties during the transport in metallic cage (Salman, personal communication). The five other collars worked from 10 to 182 days, and gave between 22 and 131 locations (Table 3.4). Due to various collar performance and programmation, the average time between two locations is very different, from 2 to 33 hours, as well as the distance between two locations, ranging from 0.17 to 2.69 km. On the other side, the average distance covered by wolves, independent from collar performance, is very similar with average of 1.9 km/day, however long the wolf was studied.

At the end of the study, the wolves have dispersed to various distances, from less than 1km to more than 163km from the release site. They have dispersed in mean south-west direction (233°±80°).

Looking at the distance in function of time, Gay, Rem and Cleopa have a curve with flats, corresponding to places where they stayed for some time, separated by more or less long distances they covered. Steffi and Prossia have more linear curve, indicating a regular distance covered per time (Fig 3.6).

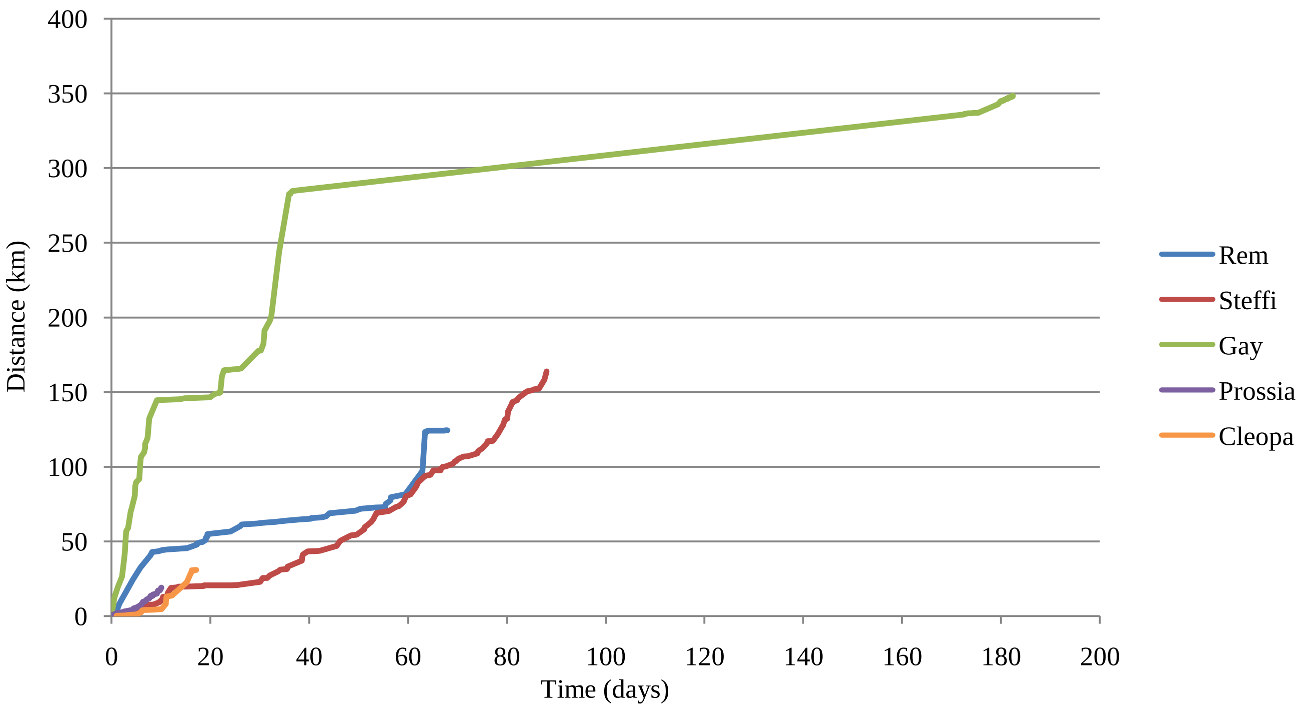
Table 3.4: General results of the 6 equipped wolves released and followed in Russia.
*For the calculation of average and standard deviation, we remove Tassia's collar that failed at the beginning of the study.

Individual	Collar ID	Date of beginning	Date of end	Number of days	Number of locations	Total distance (km)	Average distance per day (km)
Rem	53264	24/03/2010 15:28:19	31/05/2010 14:10:04	67.95	60	124.218	1.828
Tassia	53265	/	/	0	0	/	/
Gay	53266	23/03/2010 05:37:46	21/09/2010 14:01:17	182.35	131	348.402	1.911
Cleopa	55107	09/05/2010 00:38:20	26/05/2010 03:35:32	17.12	22	30.859	1.802
Steffi	61704	18/06/2010 14:05:01	14/09/2010 15:08:48	88.04	124	163.729	1.860
Prossia	98731	17/07/2010 22:37:57	28/07/2010 00:20:58	10.07	114	18.985	1.885
Average ± standard deviation*				73±69	90±47	137 ±133	1.87 ±0.04

Table 3.4 continuing.

Individual	Collar ID	Average distance between 2 locations (km)	Average time between 2 locations (days)	Ultimate direction (°)	Ultimate distance (km)
Rem	53264	2.105	1.151	218.5	39.888
Tassia	53265	/	/	/	/
Gay	53266	2.680	1.403	256.3	163.599
Cleopa	55107	1.470	0.815	328.1	9.513
Steffi	61704	1.331	0.716	271.6	3.351
Prossia	98731	0.168	0.089	90.0	0.901
Average ± standard deviation*		1.55±0.94	0.83±0.50	232.9±79.7	43.45±61.67

Fig 3.6: Distance (km) covered in function of time (day) for the 5 wolves.



3.4.2. Individual results

Collars and wolves had very different destiny and here is the chronicle of each wolf.

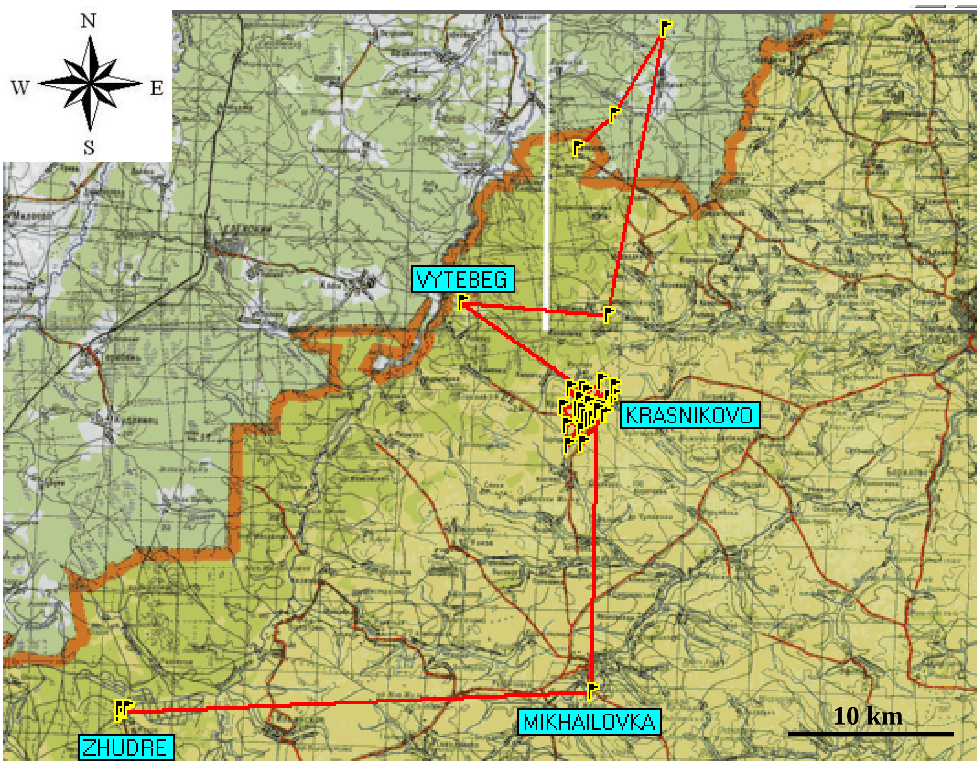
-Tassia

Although the collar was working before caging and transport, it emitted very weak signal before the release. Tassia was released anyway, hoping that the collar would recover. It did not. But the Tassia was seen later in May 2010 at several times, by the staff of the zapovednik. She was recognizable to her collar.

-Rem (Fig 3.7)

Rem was followed from March, 24th 2010 to May, 31st 2010, when he was killed close to a sheep farm near the village of Zhudre. From the release site, he started to go north-east in the forest for 8 km, before he went back 16 km south on March, 28th. Then he went straight west for 8 km to neighbourhoods of Vytebet village on March, 30th. Later he went 8km south-east to village Krasnikovo, where he stayed for more than 1.5 month (from April 1st to May 23rd). On May, 26th, he was found 16km straight south, near village Mikhailovka. The following day, he was already 26km away, straight west, near village Zhudre. He stayed there till May, 31st, when he was killed.

Fig 3.7: Movements of Rem, from 24/03/2010 to 31/05/2010.



-Gay (Fig 3.8)

Gay was followed from March, 23rd 2010 to September, 21st 2010, when his collar was found in a field. He first went 5km east from release site, near village Nagaya, then 7km straight west to village Yagodnoe the same day. The following day, he went 7km south-east to village Gorodok. On March, 25th he went 7km east then, 12.5km north, in the neighbourhood of village Kireikovo. He went 8km north-east to village Pozdnyakovo, then 11km north-west on the same day of March, 26th. The next day, he was registered near village Durnevo, 11km west from his last position, and later more 9km north-west. On March, 28th, he was localised near village Vyazovna 10km west. The next days, he went 38km north till city Sukhinichi where he was on March, 30th. Then he moved 12km south-west to the neighbourhoods of village Zhivodovka where he stayed 14 days. On April, 14th, he went 15km south near village Duminichi where he stayed 4 days. On April, 21st, he was registered 12km east and the next day he went half way back on his steps to village Polyaki, then 8km north to village Plotskoe for one day. On April 24th, he went 11km south-west, and travelled 81km west more 4 days, till the neighbourhoods of village Zhodigovichi, where he was last registered on April, 29th. The next position we got from the collar dates from September, 11th 2010, 51km south-west. Gay stayed there for 3 days, and was next registered 8km south-east in the city of Kletnya, from September 18th to 21st, date of the last position we got.

Fig 3.8: Movements of Gay, from 23/03/2010 to 21/09/2010.

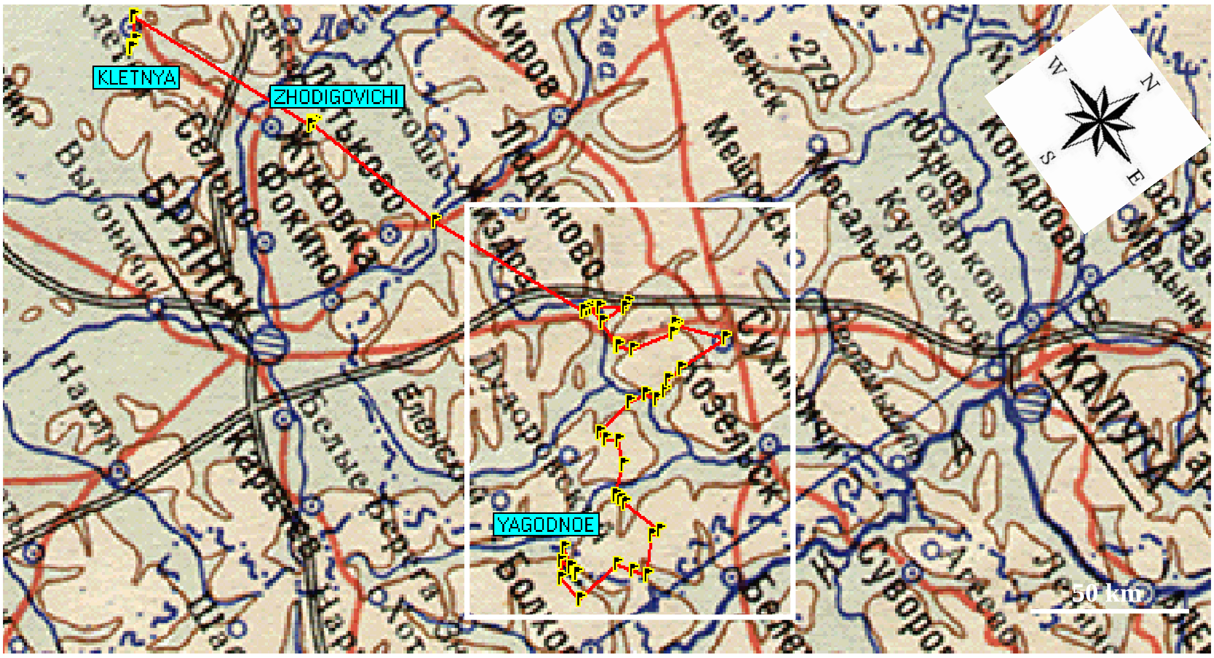
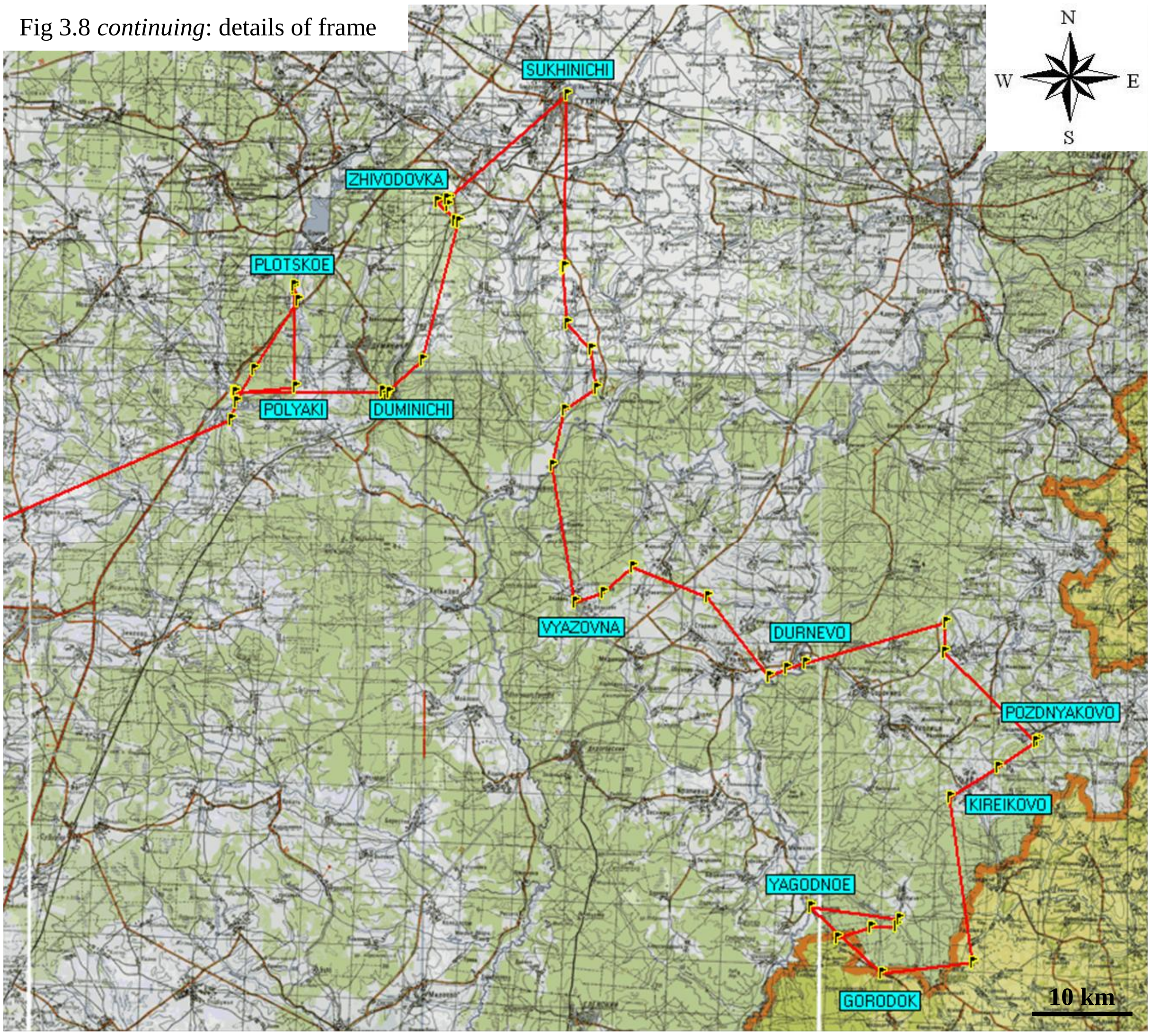


Fig 3.8 *continuing*: details of frame

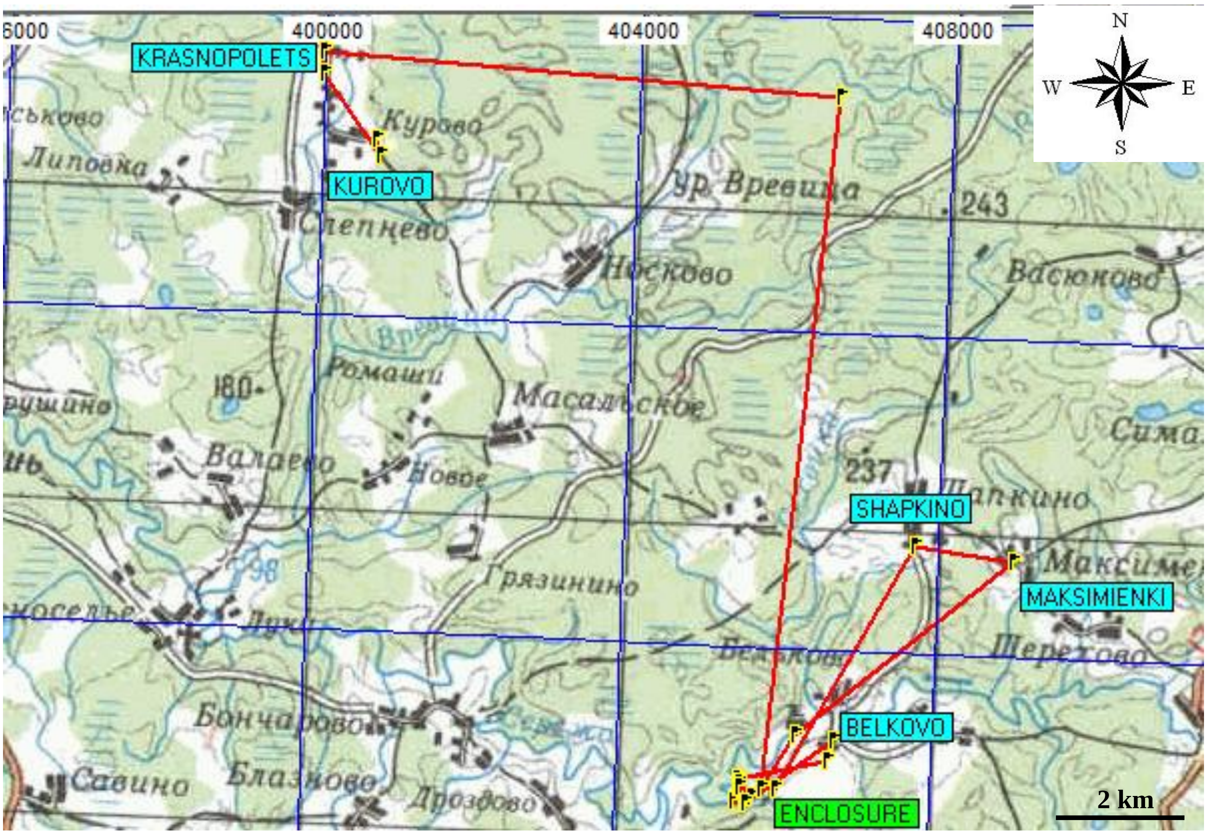


-Cleopa (Fig 3.9)

Cleopa was equipped with collar on May, 7th 2010, and went out the enclosure the following day. The first position emitted by the collar was on May, 9th 2010, and Cleopa was followed till May, 26th 2010, date of the last position received. Cleopa stayed near the enclosure till May, 14th when she was registered 1.5km farther north-east, in the field close to village Belkovo. She was even seen crossing the bridge of Belkovo at night, and ran away after she saw human (Bernard, personal communication). She spent the night in the neighbourhood and was back at the enclosure on the following day. She stayed there till May, 20th when she was localised on the road to village Shapkino (3.5km north-east from enclosure) and farther to village Maksimienki (4km north-east from enclosure) during the same night. Few hours later, she was already on her way back to the enclosure. She stayed there till May, 24th when she was found in the forest 9km away, straight north. On the following day, she was already registered 6.5km west from the last position, on the abandoned road between villages

Krasnopolets and Kurovo. Later that day, she was near Kurovo, till the last position we got from the collar on May, 26th. Investigating this last location, we found a carcass of wild boar, possibly dead in winter and dig into the ground by locals. Wolf prints were found digging it out. The last visual proof we have of Cleopa alive was August, 19th 2010, when she was seen around the enclosure, with Prossia and Steffi.

Fig 3.9: Movements of Cleopa, from 09/05/2010 to 26/05/2010.



-Steffi (Fig 3.10)

Steffi was equipped with collar on June, 18th 2010, and went out the enclosure the following day. We followed her till September, 14th 2010, date of the last position received. At first, Steffi stayed near the enclosure, till June, 22nd when she was registered in the forest, 1.7km south from the enclosure. The following day, she went close to village Belkovo, 0.7km north-east from enclosure. On June, 24th, she was back at the enclosure, and then back to her last position the following day, and stayed till June 27th. The day after, she was localised near the abandoned village Gulyaevo 0.8km west from the enclosure and later, near Belkovo. On June 29th, she was back at the enclosure, and went the following day to villages Rybino and Stepashi, 2.5km and 3km north-east from the enclosure. She went back to the enclosure at stayed there till July, 18th when she was found close to village Drozdovo, 2.5km west from the enclosure. She was back at the enclosure the next day for one day and was then localised in the forest 1.2km south from the enclosure. On July, 22nd, she was 1.4km north from the enclosure, then back there where she stayed till July, 24th. That day, she went to Belkovo, then back to the enclosure the next day, then to Rybino on July, 27th, and 2km farther north to village Shapkino. Later that day, she was localised in the forest 2km north from the enclosure, and back there for several days. On August, 2nd and 3rd, she went to Drozdovo, and back to the enclosure. The following day, she was at Gulyaevo, and to village Boncharovo, 3.5km north-west from the enclosure on August, 6th and stayed on day. On August, 8th, she was back at the enclosure, then went to Belkovo. She went to Drozdovo on August, 10th, later to the enclosure and to Gulyaevo. The following day, she was localised near Boncharovo, and on August, 13th near Drozdovo. Two days later, she was at the enclosure and on August, 16th, she was found in the forest 2km west the enclosure, on her way to Boncharovo. The next day, she went back to the enclosure. On August, 18th, she is near Belkovo, and the next day, she went to village Krasnosele, 7km north-west from the enclosure. She was near Boncharovo on August, 21st for one day and back at the enclosure till August, 24th, when she went to Belkovo and back to the enclosure. She stayed there till August, 26th when she went to Belkovo, to the enclosure and again to Belkovo the following day. On August, 31st, she was localised in the forest 2km north, then near Belkovo and at the enclosure the next day. On September, 2nd and 3rd, she went to Bonchorovo, on 4th tor Belkovo, on 5th to Boncharovo, on 6th to Stepashi then to Shapkino, on 7th to Drozdovo. Till September, 14th, she was between Drozdovo and Boncharovo. She went to Belkovo on that day and back to Boncharovo, last position we got from the collar. Steffi was seen occasionally in autumn, in Belkovo, Boncharovo, Drozdovo and Maksimienki. The last proof we have from her dates from winter (February, 20th 2011) when prints of two females of her size were found in the snow, and blood presence along the track, at breeding period.

-Prossia (Fig 3.11)

Prossia was equipped with collar on July, 15th 2010, but went out the enclosure only on July, 17th. We followed her till July, 28th 2010, date of the last position received. Prossia stayed in the close neighbourhood of the enclosure till July, 24th when the first positions about 1km south-west are registered. It seems she was travelling on the abandoned road between villages Belkovo and Gulyaevo. Later that day, she was registered on the other side of the river, 1.5km north-east from the last position, but still close to the enclosure. The following day, she back to the former position near Gulyaevo, after passing the enclosure. She went back to the enclosure on the same day and stayed in the neighbourhood for 2 days, till July, 27th when she was localised in the fields up to Belkovo. Then she went back to the enclosure and was last found in the fields up to Belkovo, 1km east on July, 28th, last position we got from the collar. Prossia was seen occasionally during summer and autumn, close to the enclosure and close to Belkovo, with her sister Steffi. She had already no collar at that time. The last proof we have from her dates from winter (February, 20th 2011) when prints of two females of her size were found in the snow, and blood presence along the track, at breeding period.

Fig 3.10: Movements of Steffi, from 18/06/2010 to 14/09/2010.

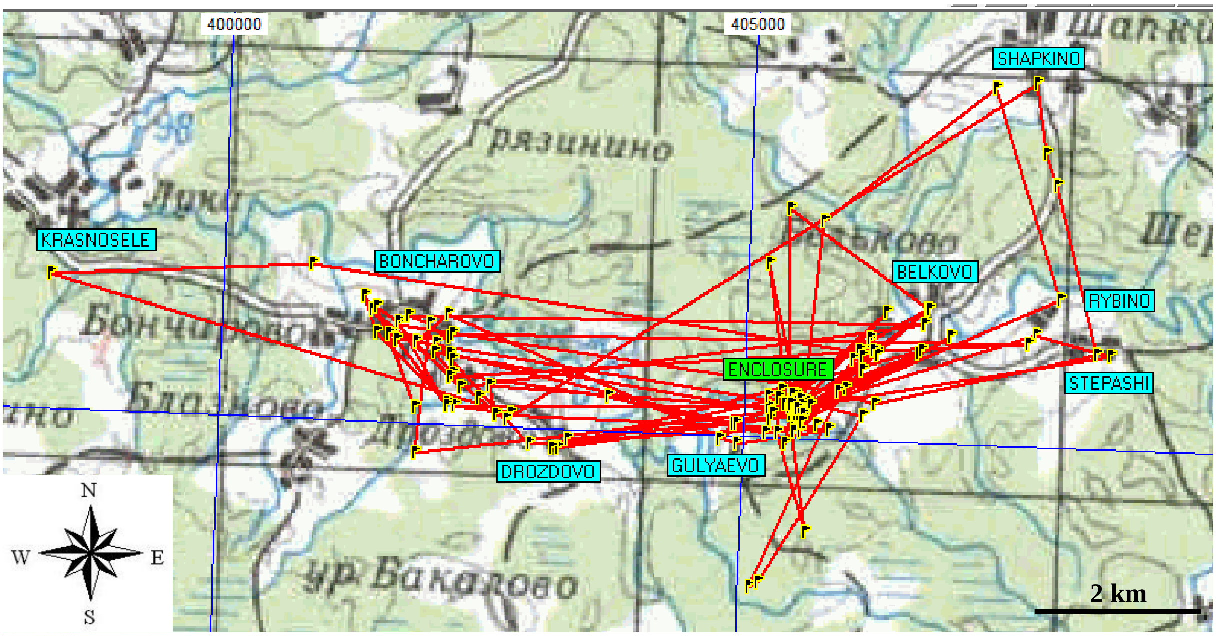
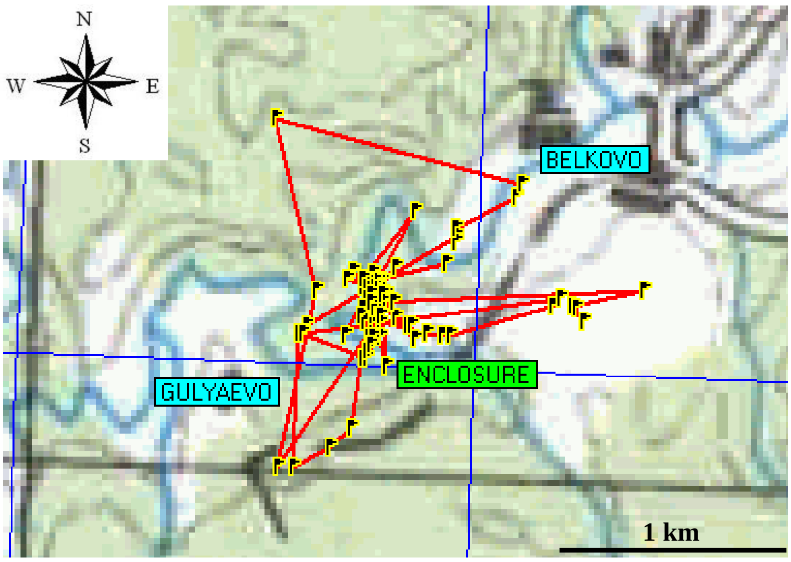


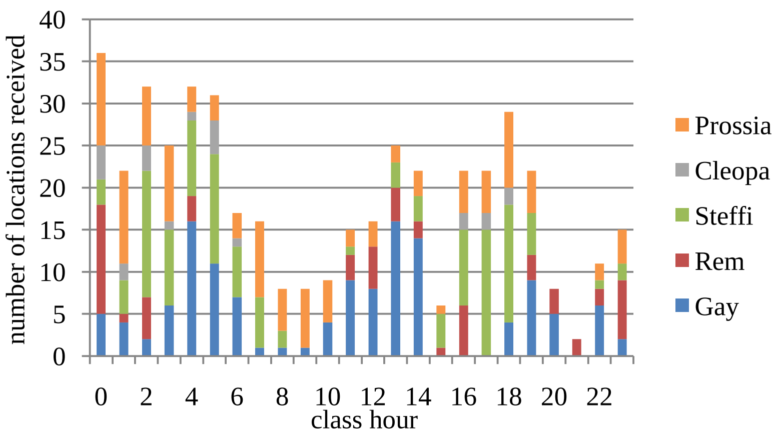
Fig 3.11: Movements of Prossia, from 17/07/2010 to 28/07/2010.



3.4.3. Collar performance

We examined the hour classes when locations were received (Fig 3.12). Those are very different from one collar to another, ranging from 0 to 16. Although collars have different programmation, some hours gave very few positions (8 to 10, 15, 20-21, with less than 10 points) and for only a couple of collars; whereas some hours gave many of them (0, 2, 4, 5 with more than 30 points; 1, 3, 13-14, 16-19 with more than 20 points) for most of collars.

Fig 3.12: Number of locations received per class hour (00:00:00-00:59:59; etc.) for each wolf.



We also examined the statistical information given by the programme Telnet, about the quality of the points and their acquisition (Table 3.5). The satellites receive a certain amount of messages (number of total points). Some messages are correct (number of good points); some have less than 7 errors and can be corrected by Telnet thanks to the method of Bose, Ray-Chaudhuri and Hocquenghem (number of points corrected (BCH)); some have more than 7 errors or were truncated and could not be corrected (number of points not corrected). Also, Telnet gives the number of points that were get over the time of acquisition (180 seconds) which reflects the poor satellite visibility or sky availability.

Table 3.5: Statistics given by the programme Telnet about points' quality and acquisition.

Collar ID	Number of total points	Number of points not corrected (% of total)	Number of points corrected (BCH) (% of total)	Number of good points (% of total)	Number of points over time acquisition (% of total)
55107	24	2 (8%)	12 (50%)	10 (42%)	0 (0%)
61704	137	13 (9%)	61 (45%)	63 (46%)	7 (5%)
98731	130	16 (12%)	69 (53%)	45 (35%)	2 (2%)

The number of fixes got after 180 seconds is quite low (< 5% of the total), presumably a good indication that the GPS receiver did not spend too much time looking for satellites, thus saving battery. About 10% of the messages received cannot be corrected, 50% of messages contains errors but are successfully corrected and only 40% of messages are free of errors.

3.5. Discussion

3.5.1. Wolves' movements

This study reported the first results after 6 months of monitoring of 6 captive-raised wolves released into the wild. The short period of collar life and the few number of animals equipped do not allow us to make quantitative conclusions, but to see some tendencies in wolves' movements after release.

Over the 3 animals "hard" released, the 2 males, Rem and Gay, went south-west at respectively 40 and 164 km away from the release site. The female Tassia, although she was not monitored because of collar failure, was observed in the neighbourhoods of the release site during several months. Her potential gestation situation could be an explication of different behaviour than the males. Indeed, we expected her to have successful breeding with one of the males, while they were still captive, as it happened the year before. In that case, at the end of March, Tassia had already passed half pregnancy time and was more likely to settle rather than travel.

It took 1 to 3 days to the "soft" released females to go out the enclosure. From our experience with previous wolves, the time spent in captivity whereas the door is opened varies largely from one wolf to another. Several reasons could explain this variability: the secure and familiar place that the enclosure constitutes as the wolves spent several months and were fed there, plus in some cases the presence of the foster mother with whom they have social relationship; on the other hand, the newly opened door is an unknown situation and thus potentially dangerous, that wolves will take some time to pass it as they do to pass fladry barrier in captivity (Musiani *et al*. 2003); and the individual difference in boldness that makes some wolves more audacious than other. These females displayed less far dispersal movements and frequent return to their raising site. They all stayed in the proximity of the enclosure for several days before they start really travelling farther. Once again, the enclosure represents a safe feeding place, with “captivity mates” still inside, a reason that make the wolves stay closer to it than exploring unknown potentially dangerous territories.

This difference in distance and behaviour of animal released with and without site acclimation is in accordance with the previous studies on grey wolves (Fritts *et al*. 2001) and red foxes (Robertson & Harris 1995). Animal “soft” released stayed near their pens at first, before wider exploring trips and returns to the release site. Animal “hard” released traveled extensively within the first weeks, with some stops for several days/weeks before exploring widely.

It is interesting to notice that the 2 “hard” released wolves, as well as Cleopa, first moved northward. Among the wolves translocated to Idaho and Yellowstone, 77% initially moved northward (Fritts *et al*. 2001). In their study, most wolves appeared to move toward home (capture site) even though they were release more than 1000 km away. And homing tendencies have been found with various translocated mammals: cougars (Belden & Hagedorn 1993, Ruth *et al*. 1998), black bears (Rogers 1988) and other wolves (Henshaw *et al*. 1979, Weise *et al*. 1975, Fritts *et al*. 1984). Homing behaviour is unlikely to happen with our wolves, either born in captivity or taken at very early age from the den. The tendency of moving southwest of all our wolves has no ready explanation and is probably anecdotic.

The 6 wolves released had dispersal movements that could be classified as “typical” for wild wolves. The oldest female, Tassia, seems to have rapidly settled, in accordance to Gese &Mech (1991) who reported that dispersing adults had a high degree of success at settling and denning. The two males, Rem and Gay, covered long distances, probably looking for food, also suggested by Boyd & Pletscher (1999), who found wolves travelling excessive distances to find suitable habitat, prey or mates, even in areas of low wolf density. The 3 young females, Cleopa, Steffi and Prossia, dispersed in steps, with returns to the familiar raising group between incursions in farther unknown territories, before they definitively left. The gradual process was described with other wolves (Potvin 1988).

3.5.2. Behaviour towards human

Looking at the geographical positions of wolves’ locations on the map, the released wolves seem appears to be very often in villages. Results should however be interpreted carefully. First, it is needed to precise that most of villages in the Russian countryside have few inhabitants or are even abandoned (Table 3.5), and are represented much more developed on the map than they are in reality. While checking some locations in the field, we found many of them more than 500 m from the closest habited house, in re-colonizing forest, while the map localized it in the middle of the village. Moreover, there could be a bias towards points in villages as single opened areas in the region, where 80% of the territory is covered by forest, and collars have been proved to work better in open area than under canopy (see Chapter. 5). Finally, according to the time, the villages were often visited at night or early morning, behaviour also encountered with wild wolves that can cross villages without being seen by humans (Bologov, personal communication).

Table 3.6: Number of inhabitants in the villages cited in the study for the wolves released at the Biological Station (source: local administrations).

Village	Nb. inhab.	Village	Nb. inhab.
Belkovo	5	Kurovo	0
Boncharovo	108	Maksimienki	2
Drozdovo	13	Rybino	4
Gulyaevo	0	Shapkino	6
Krasnopolets	51	Stepashi	6
Krasnosele	72		

However, visit of villages in order to prey on domestic animals did happen and must be discussed. The individuals Gay, Rem and Tassia clearly displayed some affinity for human (see Chapter. 1), especially at young age. That is one of the reasons why they were released only at 3 years old, waiting for them to recover wild, and why they were moved before released. Based on our experience, tame wolves may regain their wildness after certain conditions: moving to a new territory different from their raising site; or special event such as encounter with wild wolves (Bologov *et al*. 2010). Indeed wolves display cautious behaviour when in unknown territory. However, the long trips of Gay and Rem at a season when snow is still present and the small prey - rare, may have been confronted to critical energetic situation. They approach human, probably associating them with food (Henshaw *et al*. 1979). In the case of Gay and Rem, no attack on domestic animals was claimed. They may have foraged close to human settlements and used anthropogenic food sources such as garbage, hunt/slaughter remains or prey on domestic animals such as wild wolves do on disturbed territory (Fritts & Mech 1981, Salvador & Abad 1987, Theuerkauf 2003). Rem was killed after he has been seen several times in the neighbourhoods of a sheep farm, probably attracted by the smell of meat. He was killed while attempting an attack on sheep flock. He was in energetically good condition when killed. The fate of Gay remains unknown as people pretend to have found his collar. Unless he lost a lot of weight, it seems unlikely that he lost his collar so easily. But his last locations close to a city make possible the idea that he was killed by people who preferred to hide it. Steffi was seen attacking domestic animals, in particular hens, ducks and sheep. We explain her lack of human fear by several reasons (see Chapter. 4), including inter-individual differences in behaviour which makes that wolf bolder than others. Henshaw *et al*. (1979) experience 3 losses over 4 in their experimental release of captive wolves, 3 being killed by human because of nuisances, the last one being recaptured. They conclude that captive-raised wolves cannot be successfully released because they maintain their affinity for humans although they were raised without taming intention and were considered cautious to people. On the other hand, they were raised cage in 8x12m enclosures in an area of high human activity, fed by human and involved in six experiments involving human handling or close human presence (Henshaw *et al*. 1979). From our experience of raising wolves in different situations, this was more than enough to make those wolves habituated to human.

3.5.3. Recommendations for future release

This study highlights some risks of releasing captive-raised animals. Release procedures that involve no site acclimation do not give the wolves the opportunity to develop their movement, navigational and foraging skills close to a familiar secure site. Robertson & Harris (1995) recommend as well soft releases, so that red foxes could develop their survival skills. Although it seems obvious, raising enclosures should be as close as possible to natural environment, large and covered by forest/bush enough to allow a choice among different regions and to allow animals to be visually separated from human (Frézard & Le Pape 2003). The raising site should be as far as possible from human settlements and activities so as to avoid disturbance and the habituation of wolves to them. The release site would have to provide an abundance of easily-obtainable small prey, while wolves developed their ability to catch larger prey (Henshaw *et al*. 1979, Bologov *et al*. 2009). As captive-raised animals are more susceptible to human-caused mortality, effort should be made to inform the public of the nature of a transplant effort (Henshaw *et al*. 1979). We would finally conclude in the likelihood of captive-raised wolves to make successful transplant stock, but would highlight the importance to select the individuals to be released. This is important for any release program to provide behaviorally adept individuals that will survive and reproduce in the wild (Bremner-Harrison & Cypher 2007). In recent years, recognition of variation in behavior among non-human individuals has gradually increased and animal temperament became an important concept for wildlife conservation concept (McDougall *et al*. 2006). The International Academy of Animal Welfare Sciences recognizes the importance of individual variation and includes it in the factors for selection of animals for reintroduction (International Academy of Animal Welfare Sciences 1992).

3.5.4. Collar performance

The performance of the collars was lower than expected, especially concerning longevity. The estimated operational life was 1 year, but 4 of the 6 collars failed before, the last ones kept working after the collar was found (ID 53266) or the animal died (ID 53265). One collar (ID 53264) may have failed due to our negligence, when we left it in metallic cage. The other 3 collars failed after several days or weeks with unknown reason. Salman (2010) admitted that the traditional collars, with external antenna, often failed, because animals damage the antenna while fighting, scratching, climbing etc. From our observations in enclosure while testing the collars, wolves liked chewing the external device on each other and 2 antennas were cut during the tests. New models of collar with internal antenna are already tested (Salman 2010), and gave less fix per day but over a longer period.

Although satellites pass at regular intervals during the day, some times of the day are empty of fixes. Probably some satellites give better results also because of longer time over the territory or because of azimuth. Another study in Russia (Dubinin *et al*. 2010) reported lower performance of the Argos transmitters than expected with only 21% of the sessions resulted in a successful location estimate, vs. 40% of location estimate for satellite passes in an American study (Keating *et al*. 1991). It could be thus more effective to program the collar at time when satellites passes are better and so save some battery life. Keating *et al*. (1991) added that location efficiency and battery life for wolf platforms are only half those of ungulates'.

The number of locations received per day was very variable from one collar to the other, due to different programming and testing. However, even 1.5 days between two positions still gave interesting information, as our study wished to focus mostly on the long-term survival and movements of released wolves. Premature failure of GPS collars is a reality in the field (Johnson *et al*. 2002) and other researchers have reported collar failures within context of shorter studies. Moen *et al*. (1996) reported premature failure of all six prototypes Lotek placed on moose for a 12-month study. Dussault *et al*. (1999) noted that of 20 collars deployed on moose worked less than five months and thus failed prematurely. Merrill *et al*. (1998) who placed eight prototypes ATS on wolves and three on white-tailed deer for a 160 days study, had 8 over 11 premature failures. We expect that progress in technology will make the GPS collars more and more effective. Obviously, bad luck prevented us to keep on monitoring the wolves on a longer period.

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Chapter 4. Food habits of captive-raised wolves reintroduced into the wild

Chapitre 4. Les habitudes alimentaires de loups élevés en captivité et relâchés dans la nature

Глава 4. Особенности питания волков выращенных в неволе и выпущены в дикую природу

4.1. Abstract

Abstract: Many reintroduction projects exist around the world, concerning a large variety of species. Most of them do not train the animals before release, and feeding becomes a key issue in term of success. Predatory behaviour is instinctive in canids species, but their efficiency in prey-killing is also built on a learned part, usually by training with the parents. To understand how orphan captive-raised wolf pups can cope with the situation, we collected 95 scats of wolves reintroduced in western Russia between September 2010 and June 2011. We assessed their diet thanks to 4 different methods, and looked at the seasonal variations and the importance of vegetation. Wolves mainly preyed on wild boar, moose and mountain hare, which represent more than 75% of the biomass ingested. Next come various middle-sized mammals and small rodents. The average number of prey per scat is 1.4, reflecting the diversity in wolf diet. The wolves in this study also consumed a large amount of vegetal matter, and occasionally preyed on domestic animals, adapting their foraging behaviour to the seasons. These results showed again the high opportunism and adaptability of wolves and gave encouraging signs for wolf reintroductions.

Key words: *Canis lupus*, diet, reintroduction, opportunism.

Résumé : De nombreux programmes de réintroduction existent à travers le monde, concernant un large spectre d'espèces. La plupart n'entraînent pas les animaux avant le relâcher, et la recherche de nourriture devient une question clé en termes de succès. Le comportement prédateur est instinctif chez les canidés, mais leur réussite dans la mise à mort de proies est aussi basée sur une part apprise, en général en s'entraînant avec les parents. Pour comprendre comment des louveteaux orphelins élevés en captivité pouvaient s'en sortir, nous avons collecté 95 excréments de loups réintroduits en Russie occidentale, entre septembre 2010 et juin 2011. Nous avons évalué leur régime alimentaire par 4 méthodes différentes, et regardé les variations saisonnières et l'importance de la végétation. Les loups se nourrissent principalement de sanglier, élan et lièvre variable, qui constituent plus de 75% de la biomasse ingérée. Viennent ensuite différents mammifères de taille moyenne et les petits rongeurs. Le nombre moyen de proies par excrément est de 1,4 reflétant la diversité du régime alimentaire. Les loups de cette étude ont aussi consommé une grande quantité de matière végétale, et ont occasionnellement tué des animaux domestiques, adaptant leur comportement alimentaire aux saisons. Ces résultats montrent encore l'opportunisme et l'adaptabilité des loups et donnent des signes encourageants pour la réintroduction de loups.
Mots-clés : *Canis lupus*, régime alimentaire, réintroduction, opportunisme.

Абстракт: Многочисленные программы реинтродукции существуют по всему миру и по относительно широкому спектру видов. В большинстве из них животных не дрессируют перед выпуском, и кормление становится ключевым вопросом в понятии успеха. Хищническое поведение существует инстинктивно у псовых, но успех добычи также основан на обучении, обычно полученным от родителей. Чтобы понять, как выращенные в неволе щенки волков могли справиться с ситуацией, мы собрали 95 экскрементов волков выпущенных в западной России, в период сентябрь 2010 г. и июнь 2011 г. Мы оценили режим их питания по 4 различным методам, и проследили сезонные изменения и важность растительности. Волки питаются главным образом кабаном, лосем и зайцем, которые составляют более 75 % съеденной биомассы. Затем следуют различные млекопитающие среднего размера и мелкие грызуны. Среднее количество добыч по экскрементам 1.4 отражает разнообразие в питание волка. Исследуемые волки также потребляли большое количество растительности, и иногда охотились на домашних животных, приспосабливая свое пищевое поведение по

сезонам. Эти результаты показали высокий уровень адаптации щенков волка к жизни в дикой природе и дали обнадеживающие предпосылки для реинтродукции волков.
Ключевые слова: *Canis lupus*, питание, реинтродукция, адаптация.

4.2. Introduction

Reintroduction of wild animals is a tool for biodiversity conservation (Nilsen *et al*. 2007, Seddon 2007). Nowadays many vertebrate species are threatened due to the high human activity. The reintroduction of endangered species can help prevent extinction. Moreover, reintroducing wild animals is not limited to endangered species; it is also a major concern to maintain top-down regulation (Terborgh *et al*. 1999) and sustain healthy populations with enough gene flux. Many projects of reintroduction, concerning a wide variety of species, exist all over the world.

Most reintroductions neither prepare nor train the animals before release (Kleiman 1989), but some do. For example, the red wolves (*Canis rufus*) were prepared for hunting (first by exposure to carcasses and then to live prey), but the efficiency of such training has rarely been proved. According to Klein (1995), wolves bred in captivity without any previous experience, can hunt and kill wild prey and survive once released into the wild, exactly like domestic cats and dogs may instinctively do when needed. Fox (1969) reported that hand-raised canids such as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), grey foxes (*Urocyon cinereoargenteus*) as well as Artic foxes (*Alopex lagopus*) reacted to the movement of the prey which was a stimulus for orientation, approach and chase. Similarly, wolf predation behaviour would be instinctive. Badridze (2003) showed that 6-week-old hand-raised wolves play hunting with a potential prey until they bite the flesh. After this experience, they always hunt the known prey (stable formed reaction at 3 months old). Moreover, pups show very early in their development playing behaviours through fighting and chasing games by pushing the hips and shoulders like adults do for hunting, even without having been raised by their mother (Badridze 2003). Prey-killing patterns seemed to be present very early in the life of canids. After a period of experience depending on the species, catching, carrying, killing and eating sequences were present for all species at the term of their fourth month (Fox 1969). It is also through the early exploratory behaviour that canids learn where to find a prey, how to approach, efficiently catch and kill (Fox 1969). Wolves benefit to some degree from « social help » when learning with adults and being organized as a pack. Probably, the efficiency of hunting is improved while travelling with adults and imitating them especially for hunting large ungulates (Fox 1969). However, observing the feeding behaviour of twenty-two hand-raised pups from 1993 to 2008, we found that pups were able to find their own food (foraging on the ground, collecting fruit, etc…) and hunt (smaller to larger prey) without any external help from parents or adults (Becker *et al*. 2010).

Wolf reintroduction has been done in several countries: grey wolves (*Canis lupus*) in Yellowstone National Park in 1995-1996 (Northern Rocky Mountains, USA) as well as in Idhao, the Red wolf (*Canis rufus*) in Northern Carolina from 1987 to 1989 (Wayne & Gittleman 1995, Peterson 2007), and the Mexican grey wolf (*Canis lupus baileyi*) in the mountains of the Southwest USA in 1998. There was also a preliminary evaluation of possible reintroduction in Scotland (Nilsen *et al*. 2007, Boitani 2000).

Although the wolf is mainly a predator of wild ungulates (Ballard *et al*. 1987), it is also an opportunist with a generalized diet (Salvador & Abad 1987). Depending on local availability, wolves usually prey on mid-sized wild ungulates such as red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) (Ballard *et al*. 1987, Nowak *et al*. 2005). In boreal conifer forests, moose (*Alces alces*) may be an important prey species for wolves as well (Peterson *et al*. 1984). Wolves can also eat smaller prey (e.g. rodents, frogs, fish, insects) and vegetal matter (Stahler *et al*. 2006). Moreover, they may use anthropogenic food sources such as garbage or prey on domestic animals that are present in their territory (Fritts & Mech 1981, Salvador & Abad 1987, Theuerkauf 2003, Nowak *et al*. 2005).

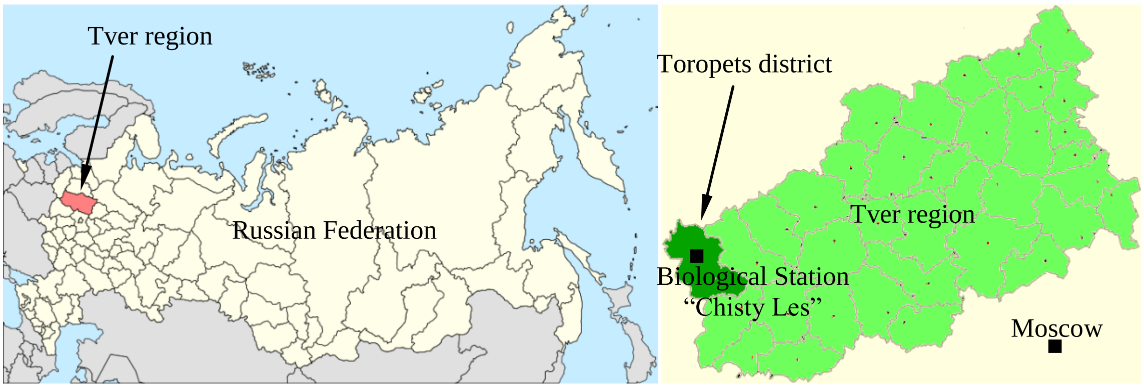
Few studies on reintroduction of hand-raised wild animals report the release success or failure (Kleiman 1989). The release is considered a success when the released animals are able to survive on their own: hunt successfully, become self-sufficient, avoid human activities, acquire the behaviour repertoire of their species (van Dijk 2005, Grundmann 2006) and reproduce (Cayford & Percival 1992). The aim of this experimental study was to follow the wolves after their release into the wild and assess their survival chances. The focus was on their food habits, evaluated via different methods of scat analysis. According to previous findings on successful releases, we hypothesized that the released wolves would be able to survive on their own without previous fastidious training. The wolves would have to find food, disperse, and look instinctively for unoccupied territory (Rothman & Mech 1979, Fritts & Mech 1981) where food was available. The lack of precise information on released wolves' food habits has induced a wide range of opinions and speculations concerning the feasibility of such project. Precise diet analyses of captive-raised wolves reintroduced into the wild would be very helpful in regard to public opinion and scientific community.

4.3. Material and methods

4.3.1. Study area

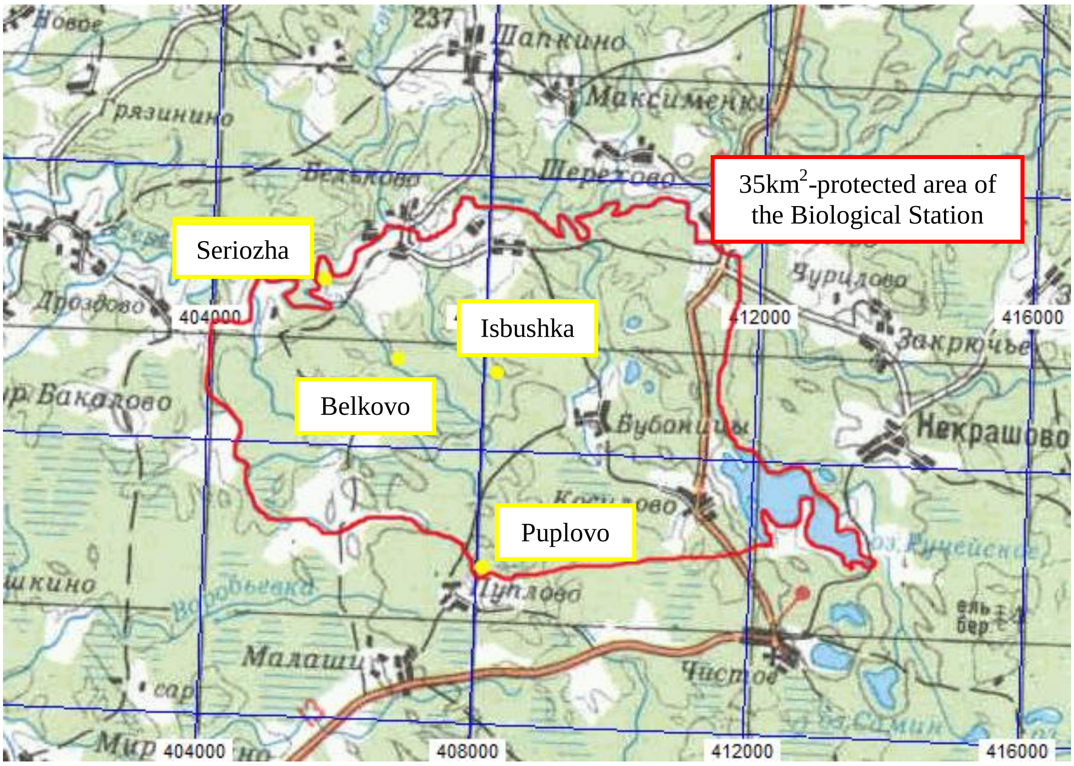
The study took place at the Biological Station “Chisty Les” (56°44’N, 31°31’E) situated 450 km north-west from Moscow, in the district of Toropets (3373 km^2), in the region of Tver, in Russian Federation (Fig 4.1). The main part of the study area was within the 35 km^2 protected area of the Biological Station, where are implanted our 4 wolf enclosures (Fig 4.2).

Fig 4.1: Situation of the Biological Station “Chisty Les” in Russian Federation.



80% of the area is covered by unspoiled southern boreal forest mainly composed of birch *(Betula pendula)*, pine *(Pinus sylvestris)* and spruce *(Picea abies)*. There are few human settlements and roads. The human density is low (6.5 inhabitants/km^2) due to a steady and constant decline in the local population since the collapse of the Soviet Union in 1990. However human disturbance is present through various activities: meat factory, timber exploitation, husbandry, traffic and hunting. Small villages and farms where the dominating livestock are hens, sheep, pigs, cows and horses, in order of importance, characterize the local community.

Fig 4.2: The 4 wolf enclosures within the protected area of the Biological Station.



The climate is continental with two main seasons, winter and summer. Temperatures vary between -40°C and +40°C. Permanent snow cover is present from November to April, with one meter depth average. Annual precipitations are important with 550-750 mm.

According to our monitoring results, no breeding wolf pack lives on the territory of the Biological Station. The closest breeding pair lives 10km away and seldom crosses the car road. Therefore the territory is mainly visited by lonely wolves released in the previous years. The wolf average density in Toropets district is 3.9 animals/1000km^2 (Russian hunting office sources for 2006).

The other large predator species present on the study area are brown bears (*Ursus arctos*) and lynx (*Lynx lynx*). The main prey killed by wolves in Russia is ungulates: wild boar (*Sus scrofa*) and moose (*Alces alces*) whereas roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) are seldom and no present in the study area. Middle mammals such as mountain hare (*Lepus timidus*), beaver (*Castor fiber*) and racoon dog (*Nyctereutes procyonoides*) may also constitute a prey choice. Wolves also prey on a variety of micro-mammals (mice and rats (Family: Muridae), voles (Family: Cricetidae, shrews (Family: Soricidae)).

4.3.2. Individuals studied

A total of 16 wolves have been released just before and during the study period (Table 4.1). However, according to our monitoring, the excrements collected mainly came from 7 of them (Cleopa, Steffi, Prossia, Apache, Cheyenne, Riksha and Raksha).

Table 4.1: Name, sex, year of birth, origin, raising method, enclosure, and date of release of the 16 wolves reintroduced during the study period.

Individual	Sex	Birth	Origin	Raising method	Enclosure	Equipment	Release
Zephir	M	2009	Zoo	Feeder	Belkovo	No	03/05/2010
Mistral	M	2009	Zoo	Feeder	Belkovo	No	03/05/2010
Alize	F	2009	Zoo	Feeder	Belkovo	No	03/05/2010
Boree	F	2009	Zoo	Feeder	Belkovo	No	03/05/2010
Cleopa	F	2009	Hunter	Foster	Seriozha	Yes	09/05/2010
Steffi	F	2009	Hunter	Foster	Seriozha	Yes	18/06/2010
Prossia	F	2009	Hunter	Foster	Seriozha	Yes	15/07/2010
Apache	M	2010	Zoo	Feeder	Belkovo	No	27/09/2010
Cheyenne	M	2010	Zoo	Feeder	Belkovo	No	27/09/2010
Nyu	F	2009	Private	Feeder	Puplovo	No	01/03/2011
Tor	M	2010	Zoo	Foster	Puplovo	No	01/03/2011
Issa	F	2010	Zoo	Foster	Puplovo	No	01/03/2011
Yamal	M	2010	Zoo	Foster	Puplovo	No	01/03/2011
Vaia	F	2010	Zoo	Foster	Puplovo	No	01/03/2011
Riksha	F	2010	Private	Feeder	Isbushka	No	20/03/2011
Raksha	F	2010	Private	Feeder	Isbushka	No	20/03/2011

The wolves came from hunters (from the neighbouring regions of Smolensk and Pskov), from zoos (Saint-Petersburg, Yaroslavl, Veliki Ustiug) and from private people. They arrive at the rehabilitation wolf centre of Biological Station between 2 weeks and 1 year old and are raised following two different methods:

-Feeder: he/she feeds the pups without direct contact as they are afraid of human.

-Foster: the pups are introduced to an adult female who behaves like their mother.

The wolves are kept in enclosures of 0.5 to 1.5 ha for several months. They are provided with food 2-3 times per week, with average amount of 1kg/wolf/day. The food provided is mainly meat from the slaughterhouse (chicken, pork, beef and horse), road kills (hare, birds), remains of hunting (wild boar, moose) or fish (whiting, cod, pout). No live prey was provided during the raising. However, in the enclosure, the wolves may catch small prey (insects, frogs, birds, rodents) and eat vegetation available (grass, berries). After release, supplemental food (carcasses mainly composed of bones and little meat) was regularly provided temporarily at enclosure Seriozha as a support for the newly released wolves.

4.3.3. Data collected

Wolf scats have a diameter equal or over 2 cm and are usually 10-20 cm long. They are composed of several cigar shaped pieces. Smell and colouration are characteristic. Faeces are essentially composed of hair and bones still visible on the surface. A total of 95 scats were collected between September 2010 and June 2011. Most of them were collected during the snow period (November-April) when wolf prints were easily found and the tracks followed. In autumn and spring, scats were collected on roads and forest trails used by wolves. The faeces were stored in labelled plastic bags and identification code was attributed, as well as the GPS location. The type of deposit site, date, sign of wolf activity and any scat characteristic were reported. The faeces were frozen prior to further treatment and analysis.

The scat was soaked in water for 24-48 hours with a few drops of dishwashing liquid to aid dissolution. Next, scats were hand separated and washed through a sieve with a mesh size of 0.5 mm in order to separate the macro components. All was rinsed with clear water into another basin. These steps were repeated the number of times needed to obtain clear distinction of the elements. Food remains retained in the sieve (e.g. hair, bones, vegetation, seeds) were separated from each other using metal tongs. All was placed in an aluminium box that was stored on the oven until complete dehumidification so as to conserve the components. Each macro element was arranged in a plastic bag and conserved until further analysis.

The analysis consisted in identifying the macro components of each scat thanks to the characteristics of each animal species with the help of reference manual (Teerink 1991) and samples collected from local hunters. The macroscopic remains of vegetation, invertebrates, and birds were identified by comparison with reference material and books (Fitter *et al*. 1991, 1997). The microscopic fraction was discarded assuming that it came from the same macroscopic food items, in the same proportions, and that it would not significantly affect the results concerning the wolf diet (Ciucci *et al*. 1996).

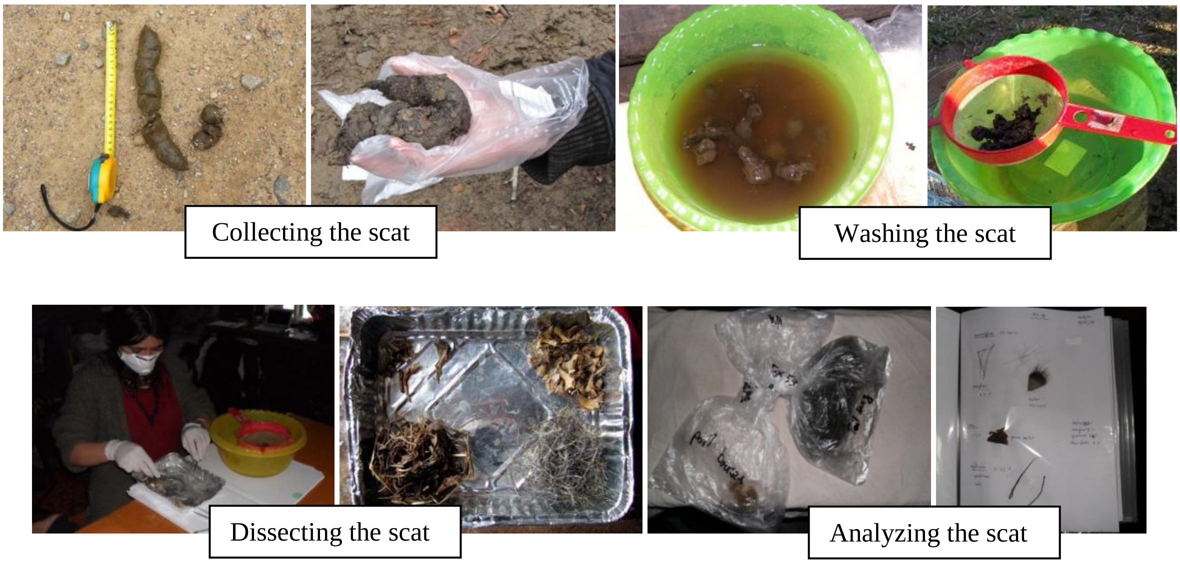
Once identified, the elements were pooled into the following categories:

Moose / wild boar / badger / fox / racoon dog / beaver / mountain hare / micro-mammals (Muridae, Cricetidae, and Soricidae families) / carrion / sheep / hen / duck / wild birds (passeriformes, galliformes, falconiformes) / insects / graminae / fruit and seeds / other plant items / others.

The latter category represents non-food items like strings, stones, leather and plastic. The elements were distributed in different classes according to their relative volume, visually estimated and expressed as a percentage of the volume of each scat (Fritts & Mech 1981, Ciucci *et al*. 1996).

The complete protocol is illustrated in Fig 4.3.

Fig 4.3: Protocol of scat collecting, preparing and analysing
(Photos: L. Becker, L. Bourg, C. Fraissard, A. Keibler).



4.3.4. Data analysis

Four different methods were used to assess wolf diet. Most studies on diet use different methods for analysing data (Ciucci *et al*. 1996, Spaulding *et al*. 1997, Andersone & Ozolins 2004) due to limitations of each method in describing at the same time the quantity and the quality of components found in scats.

We did not include in the analysis the remains of a negligible proportion in order to reduce the bias of trace amounts of food items such as long hair from ungulates or feathers that might have been trapped by the stomach from an earlier meal and also to reduce the "equating of occurrences bias" (Ciucci *et al*. 1996, Huitu 2000). This would be when food items contributing different quantities to a scat's volume are equated by frequency (Ciucci *et al*. 1996).

The frequency of occurrence (FO) was assessed and calculated as percentage of the total number of occurrence of all food items and of the total number of scats (Ciucci *et al*. 1996). It expressed the frequency of a food item relative to the other food items present in the scat as well as the frequency of a food item present in the total of scat collected. The frequency of the different prey items could be expressed independently by group (e.g. mammals, ungulates, mustelids) (Kelly 1991).

When the scats analysed contained more than one item, we visually estimated the fraction of each prey item found in each scat and summed these fractions to give the equivalent number of scat (n) representing a particular prey type (Floyd *et al*. 1978, Spaulding *et al*. 1997, Ciucci *et al*. 1996). We called it REB (Relative Estimated Bulk) as Spaulding et *al*. (1997) did in their study and expressed it as percentages.

Biomass ingested (n*y) was calculated thanks to the REB to override the bias associated with small prey items and when there is more than one prey type per scat (Floyd *et al*. 1978, Fritts & Mech 1981). To estimate the weight of live prey eaten per scat (y), we used Weaver's (1993) equation where the independent variable (x) is the live weight (kg) of the prey recovered in the scat:

$$y = 0.439 + 0.008\,x$$

Body mass of the live prey species was taken from literature (Corbett 1989, Aulagnier *et al*. 2010). The product (n*y) expressed in kilograms is the total weight of each prey type consumed (i.e. biomass) by the wolves during the study period (Corbett 1989).

Statistical analysis was performed with the software SPSS Statistics 19.0. The results obtained by each scat-analysis method (% FO/scats, % FO/items, % REB, % and kg Biomass) of faeces data were expressed as ranks of the food items by ascending order (Corbett 1989, Ciucci *et al*. 1996). Pearson's correlation coefficients (r) were also calculated to test for differences between pairs of methods (Corbett 1989, Spaulding *et al*. 1997, Ciucci *et al*. 1996). The coefficient ranges between 1.0 (perfect positive correlation) and -1.0 (perfect negative correlation). The closer r is to +1 or -1, the stronger the likely correlation. A significant value of r ($p < 0.01$) was assumed to indicate that there were no significant differences between methods and that all methods could be used for assessing wolf diet (Spaulding *et al*. 1997). Seasonal variation by comparing the FO of selected food items was tested using Chi-square test.

4.4. Results

4.4.1. General diet

A total of 95 wolf scats were collected from September 2010 to June 2011 on the area of wolf release (Fig 4.4). Average number of prey types found per scat was 1.4±0.8 with a variation from 0 to 4 prey types per scat. Most of scats contained one (48%) or two (33%) prey types, whereas three prey types were recorded in 7% of the studied material. 11% of the faeces did not contain any prey item (but carrion), and a single scat (1%) contained four different prey types simultaneously (Fig 4.5).

Fig 4.4: Locations of the 95 wolf scats found between September 2010 and June 2011.

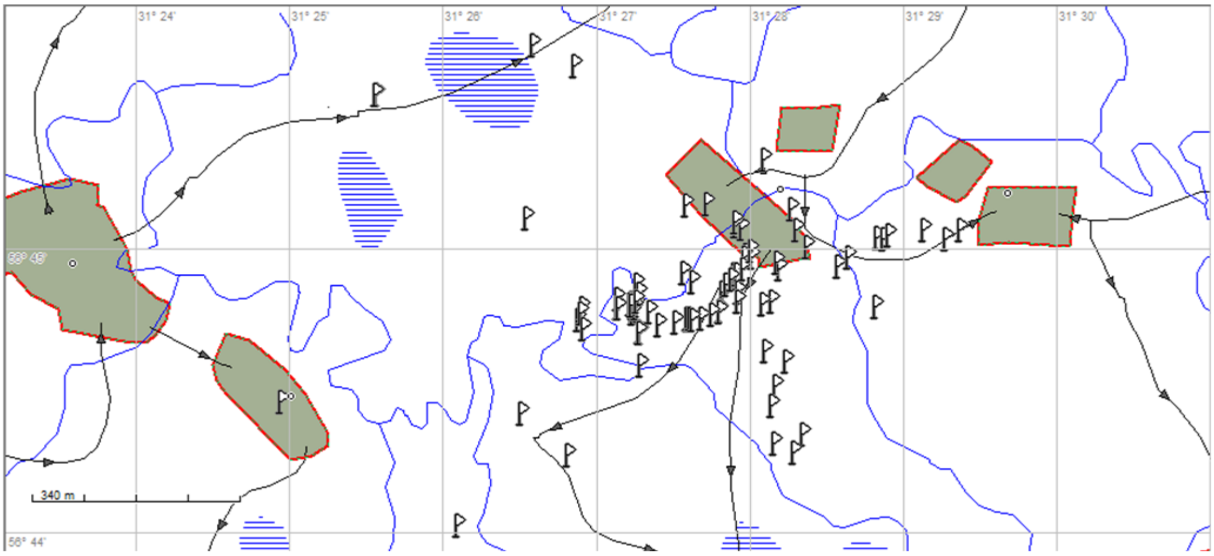


Fig 4.5: Number of prey items found per scat

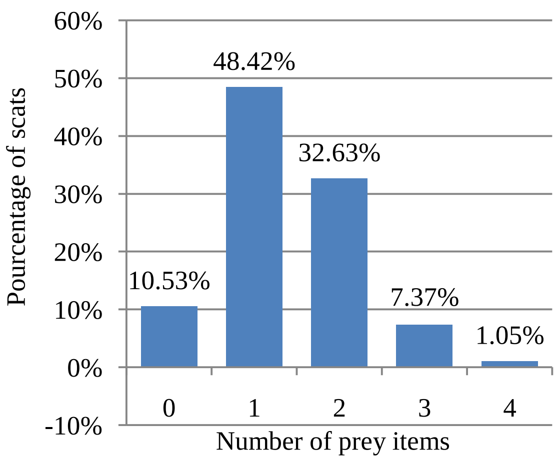
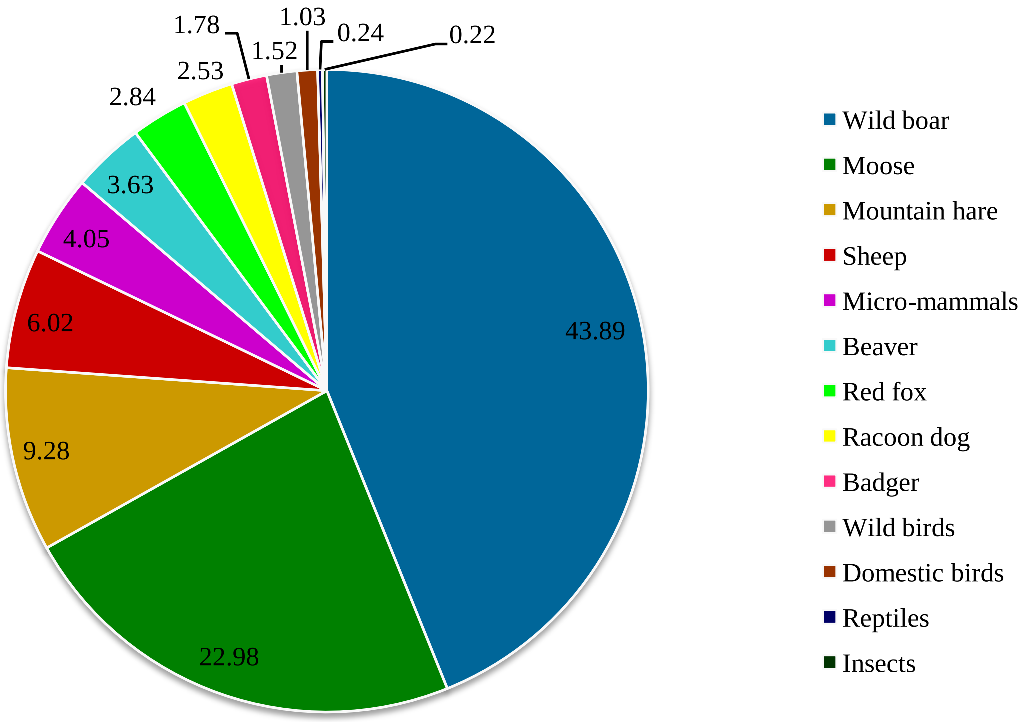


Table 4.2: Diet of captive-raised wolves released in Russia, analyzed by 4 methods.
FO/scats is the frequency of occurrence of an item in the total number of scats. FO/items is the frequency of an item relative to the other food items found in scats. REB is the average volume of an item per scat. Biomass is the equivalent prey mass consumed. For the calculation of FO/items, REB and biomass, we did not take into account the non-feeding items *i.e.* carrion, graminae, other plants, other.

Food items	**FO/scats**			**FO/items**		**REB**		**Biomass (Weaver)**		
	N	**%**	**Rank**	**%**	**Rank**	**%**	**Rank**	**Kg**	**%**	**Rank**
MAMMALS										
Moose (*Alces alces*)	19	20.00	3	9.79	3	5.59	4	17.09	22.98	2
Wild boar (*Sus scrofa*)	39	41.05	1	20.10	1	18.68	1	32.64	43.89	1
Sheep (*Ovis aries*)	6	6.32	10	3.09	10	4.20	7	4.46	6.02	4
Beaver (*Castor fiber*)	5	5.26	11	2.58	11	4.37	6	2.70	3.63	6
Badger (*Meles meles*)	4	4.21	12	2.06	12	2.53	10	1.32	1.78	9
Racoon dog (*Nyctereutes procyonides*)	8	8.42	7	4.12	7	4.00	8	1.88	2.53	8
Red fox *(Vulpes vulpes)*	7	7.37	8	3.61	8	4.57	5	2.11	2.84	7
Mountain hare *(Lepus timidus)*	24	25.26	2	12.37	2	15.54	2	6.90	9.28	3
Micro-mammals	16	16.84	4	8.25	4	7.21	3	3.01	4.05	5
CARRION	12	12.63	-	6.19	-	9.67	-	-	-	-
BIRDS										
Domestic (hen, duck)	7	7.37	9	3.61	9	1.77	11	0.76	1.03	11
Wild birds	13	13.68	5	6.70	5	2.64	9	1.13	1.52	10
REPTILES	4	4.21	13	2.06	13	0.43	12	0.18	0.24	12
INSECTS	12	12.63	6	6.19	12	0.40	13	0.17	0.22	13
VEGETAL MATTER										
Graminae	65	68.42	-	-	-	-	-	-	-	-
Fruits and seeds	18	18.95	-	9.28	-	2.82	-	-	-	-
Other plants	83	87.37	-	-	-	-	-	-	-	-
OTHER	17	17.89	-	-	-	-	-	-	-	-

Fig 4.6: Percentages of biomass consumed and calculated using Weaver's equation (1993).



The relative importance of food items found in the scat sample was quantified by four different methods (Table 4.2). The food items were ranked in ascending order according to the methods assessing the diet. The methods show the same top three prey consumed: moose, wild boar and mountain hare representing more than 75% of the biomass consumed. There is a clear dominance of wild boar found in more than 40% of scats. The top three were followed by middle (beaver, red fox, raccoon dog, badger) and micro-mammals, and domestic sheep, together representing more than 20% of the biomass consumed. Birds, insects and reptiles were seldom consumed and constitute only 3% of the biomass (Fig 4.6).

The carrions were not included in the ranking as they were mainly made of bones and were of poor feeding interest. Carrions were given as supplement and attraction during the winter and were typically distinguished by the presence of cattle bones in the scat without any hair and the scat itself was of a particular consistence. Twelve scats out of 95 were constituted of carrion (12.6% of occurrences per scats but 6.1% of occurrences per items). The category “other” that gather non-feeding items such as stone, paper, plastic, string, sponge, and rubber was not included in the ranking either, although they were found in 17% of scats. The vegetal matter is treated below.

Agreement between methods was significant in all pair-wise comparisons ($0.78 \leq r \leq 1.00$, $p<0.01$) (Table 4.3). The lowest significance was for the correlation involving the REB method and was higher when involving the frequency per scat. Accordance among the different methods for ranking was particularly strong for the highest and the lowest ranks (i.e. $4 \geq$ rank ≥ 10), with some variations with the biomass model and the REB method.

Table 4.3: Pairwise comparisons between 4 methods of scat-analysis to assess released-wolves diet in Russia (Pearson correlation coefficient, r)

		FO/items	REB	Biomass
FO/scats	Correlation coefficient Significance N	1.000 .000** 13	.885 .000** 13	.870 .000** 13
FO/items	Correlation coefficient Significance N	-	.885 .000** 13	.870 .000** 13
REB	Correlation coefficient Significance N	. -	-	.780 .002** 13
** Correlation is highly significant at the 0.01 level (p<0.01).				

4.4.2. Vegetal part

Vegetal matter was classified in three categories: graminae, fruits and seeds and other plant items. The latter category gathers the leaves, stems, wood, and buds of plants.

Graminae were found in 65 scats over 95 (68%), with an average proportion of 10%. Fruits and seeds occurred in 18 scats (19%) at an average proportion of 13%. Apple was found 6 times (6%), plum twice (2%), rowan, watermelon, sunflower and hazelnut once (1%). Seeds of *Myrrhis odorata*, *Heracleum sphondylium* and an unidentified one were found in 3 scats (3%). Other plant items were found in 85 scats over 95 (87%) with an average proportion of 8.49%. Spruce and pine needles frequently occurred (67%) as well as leaves of various species (59%). Pine buds were found 10 times (11%), sphagnum 5 times (5 %) and birch bark 4 times (4 %) (Table 4.4).

Table 4.4: Frequency and proportion of vegetal matter; species of fruits, seeds and other plant items found in scats.

	Graminae	Fruits and seeds[a]	Other plant items[b]
% FO/scats	68.42	18.95	87.37
Average proportion when present (%)	10.44	13.22	8.49
Species [a] (% FO/scats) [b] (part found) *identification currently proceeding at the Botanical Institute of Strasbourg University		*Malus sylvestris* (6.32) *Myrrhis odorata* (3.16) *Heracleum sphondylium* (3.16) Unidentified* (3.16) *Prunus domestica* (2.11) *Sorbus aucuparia* (1.05) *Corylus avellana* (1.05) *Helianthus annuus* (1.05) *Citrullus lanatus* (1.05)	*Picea abies* (needle) *Pinus sylvestris* (needle, bud) *Betula pendula* (leaf, bark) *Sphagnum pallustre* (whole) Lichen (whole) *Equisetum sp.*(whole) *Ledum sp.*(leaf)

4.4.3. Seasonal variation

We used the biomass method and gathered the food categories in the following classes to proceed to seasonal analysis:

-Wild ungulates (moose, wild boar)

-Middle mammals (badger, beaver, raccoon dog, red fox)

-Micro-mammals (Muridae, Cricetidae, and Soricidae families)

-Wild birds (passeriformes, galliformes, falconiformes)

-Invertebrates (reptiles, insects)

-Domestic animals (sheep, domestic birds)

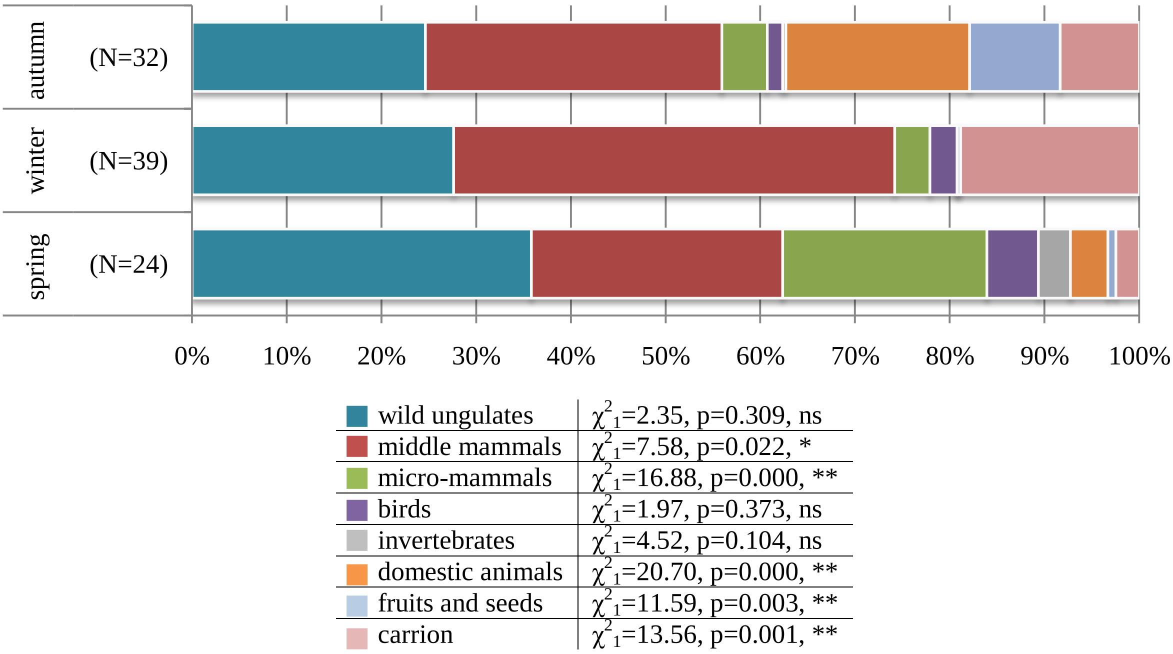
-Fruits and seeds

-Carrion

Over a total of 95 scats, 32 were collected in autumn (01/09/2010-31/10/2010), 39 were collected in winter (snow period, 01/11/2010-15/04/2011), and 24 were collected in spring (16/04/2011-15/06/2011).

Fig 4.7 shows the proportion of each class according to the season, and the results of comparison (Chi-square test). There is no significant difference in ingestion of wild ungulates, birds and invertebrates depending on the season (p>0.05). They are respectively consumed at average of 24.73%, 2.81% and 1.06%. Middle mammals are consumed about twice more in winter (41.64%) than in autumn (24.56%) or spring (22.29%) ($\chi2=7.58$, $p<0.05$). Micro-mammals are found mostly in spring (18.13% vs. 3.75% and 3.33%) ($\chi2=16.88$, $p<0.01$), whereas domestic animals and fruits and seeds are consumed mostly in autumn (respectively 15.22% vs. 0% and 3.33%, $\chi2=20.72$, $p<0.01$; and 7.5% vs. 0.28% and 0.71%, $\chi2=11.59$, $p<0.01$). Finally, carrions were consumed mostly in winter (16.90% vs. 6.56% and 2.08%) ($\chi2=13.56$, $p<0.01$).

Fig 4.7: Seasonal analysis of the diet (biomass method, %) of released wolves.
Autumn: 01/09/2010-31/10/2010, winter: 01/11/2010-15/04/2011, spring: 16/04/2011-15/06/2011. Chi-square test: **: p<0.01, *: p<0.05, ns: p>0.05.



4.5. Discussion

4.5.1. Opportunistic wolves

The present study offers preliminary insights into the feeding ecology of reintroduced wolves into the wild in Russia. It presents the first indication of diet composition of orphan captive-raised wolves. Many prejudices would suggest that captive-raised carnivores lack fear of human and are likely to prey on livestock. This study however showed that reintroduced wolves are opportunistic carnivores. Their diet is mostly composed by wild mammals and only few scats contained remains of domestic animals.

Wolves' opportunistic characteristic is described in various studies where wolves living close to human settlements may use anthropogenic food sources (i.e. garbage) and domestic animals (Fritts & Mech 1981, Salvador & Abad 1987, Theuerkauf 2003, Nowak *et al*. 2005). The paper, plastic, string, rubber and sponge occasionally found in their excrements were thus probably ingested by accident when foraging on garbage. The seeds of watermelon and sunflower found in the excrements were very likely eaten while foraging close to villages, as these plants do not grow in the area. But watermelon is often consumed in summer and seeds of sunflower are typically eaten by Russians. Empty sunflower seeds packing were found in the forest attesting their consumption by foresters.

In this study, domestic animals represented 7% of the biomass ingested with the main proportion attributed to sheep (6%) and the rest to hen and duck. In western and southern Europe, many authors reported a high dependence of wolves on livestock, mainly on sheep, goats, cattle and horses in summer (Salvador & Abad 1987, Cuesta *et al*. 1991, Meriggi *et al*. 1996, Poulle *et al*. 1997, Vos 2000). In northern and eastern Europe, the attacks happen mainly in winter and target dogs (Sidorovich *et al*. 2003, Andersone & Ozolins 2004, Kojola *et al*. 2004). Here, depredation on domestic animals happened mostly in autumn, and were conducted by two of the released wolves, Steffi and Prossia. Steffi especially was sometimes observed very close to villages, and some attempts of attack were even stopped by human. Wolves can be highly tolerant of human activity and live very close to human settlements by habituation (Wam 2002, Theuerkauf 2003). Moreover, three factors could explain Steffi's lack of human fear:

-the individual behavior of that wolf, who is very bold in comparison to wolves we had before

-the environment where she was kept before we took her to the centre (a house in a big village, in contact with human and dogs)
-the enclosure where we kept her for several months (so as to treat her against got mange mite, she was moved to a smaller enclosure where she had no possibility to hide anymore and was in close distance to human).
Large individual differences in reaction to threats may be explained by genetic environmental influences (Boissy 1995). Individual rehabilitated brown bears also displayed differing reactions to humans (Djuro 2005). A genetic component in reactivity to humans has been found in several domestic species (poultry, pigs, sheep and dogs) (Dickson *et al*. 1970, Goddard & Beilharz 1984, Jones 1986, Hemsworth *et al*. 1990, Jones & Waddigton 1992). The influence of genetic factors on psychobiological reactivity seems to be consistent in different adverse situations and also over time (Brush *et al*. 1985).

Attacks were grouped in the summer months (August, September) and happened on unprotected flocks. They seemed to stop after several human interventions and shots to scare the wolves. Later, as soon as the first snow falls all animals were kept inside for the winter months, so attacks no longer happened.

4.5.2. Comparison with wild wolves' diet

The diet of our released wolves is mainly composed of wild ungulates, in accordance with many studies on wolf food habits (Okarma 1997, Jedrzejewska & Jedrzejewski 1998). While hoofed mammals are the base food resource of wolves, the species preyed differs, mostly depending on the density or the probability of occurrence. Thus, red deer are the most hunted prey in the most part of Europe (Jedrzejewska & Jedrzejewski 1998), while it is moose in Finland (Gade-Jorgensen & Stagegaard 2000), roe deer in Germany (Ansorge *et al*. 2006) and wild boar in Italy (Capitani *et al*. 2004).
Although moose is said to be the main prey in boreal forest (Bibikov 1982) and wild boar avoided (Jedrzejewska *et al*. 1994, Okarma *et al.* 1995), our study shows that wild boar represents the majority of biomass consumed (44%). Several theories have explained the preference/avoidance of wild boar. The increase of wild boar in wolf diet in time (Rusakov & Timofeejeva 1984, Mattioli *et al.* 1995) suggests a delay of reaction to the demographic changes of the species (Mech & Carns 1977, Gasaway *et al*. 1983). According to the foraging theory (Stephens & Krebs 1986), all ungulate species should have roughly the same energetic

profitability. However, wild boar meat is rich of fat (Stribling *et al*. 1984) and may thus have a higher energetic value than cervids (Valdmann *et al*. 1998). It was also proposed that wild boar was selected for its vulnerability and its availability in groups in comparison to roe deer or moose (Mattioli *et al*. 1995). Wild boars were particularly vulnerable in the last two winters where frost and snow cover were very important. I encountered several times wild boars unable to escape quickly in the high fresh snow, and local people found several dead animals, probably from tiredness or starvation. On the contrary, moose have long legs adapted to high snow cover and they often defend themselves against wolves by dangerous kicking. The particularly high proportion of moose in the food diet of released wolves may be explained by scavenging on remains of hunters or poachers. Indeed, most of the moose hairs were found in scats together with sheep hairs. If the wolves were able to hunt a moose, they would have unlikely preyed on sheep also. Scavenging also reflects the opportunism of wolves.

We noticed a high diversity in the scats collected, first in the number of different items found in total (14 prey species, plus carrion and vegetal matter), and in the number of different items found per scat (from 0 to 4, average 1.4). In most of the studies on wolf diet, the food items do not exceed 10 and there are a large proportion of scats (more than 80%) with a single item (Mattioli *et al*. 1995, Gade-Jorgensen & Stagegaard 2000, Ansorge *et al*. 2006). Zunna *et al*. (2009) made an interesting observation by comparing diet of adult and young wolves. Adults preyed only on 3 ungulate species, whereas young wolves (up to 2 years old) preyed on 6 different species including smaller mammals and birds. The explanation could be that young wolves only receive the remains of the pack hunts and thus need complement. As they are less experienced than adults, they fail at hunting big ungulates but succeed in the catch of smaller prey. Small wolf groups and solitary wolves are face to the same situation and are forced to feed more intensively on small rodents, and middle mammals (Valdmann *et al*. 1998). Our released wolves are both young and solitary and often preyed on small and middle-sized animals (27% of biomass ingested).

Looking deeper into the seasonal variations of our released wolves' diet, we noticed "steps", with first mainly sheep and moose consumed, than beaver and raccoon dog, than wild boar and hare, and finally micro-mammals and reptiles. This could suggest a progressive specialization of the released wolves. From our observation in the field, wolf pups will learn with experience and training and acquire the skills to catch prey (Becker *et al*. 2010). When they succeed in hunting an animal, they may specialize in this prey. Following 3 groups of dispersing yearlings in the wild, Bologov (personal communication) observed clear specialization: one group survived on moose remains from hunters, one group followed the river and kept hunting beavers, one group killed domestic dogs in villages. This suggests an empirical way of learning hunting. When wolf finds an easy way to get food and succeeds in it, it will keep on that way. In our case, sheep and remains of moose were easily available in summer, beaver and raccoon dog were fat and slow in autumn, wild boar and hare were vulnerable in winter, micro-mammals and reptiles were abundant and sufficient in spring. This shows again the high opportunism and adaptability of wolves. Our work and succeed in releasing captive-raised wolves that are able to find food on their own are based on these two characteristics of the predator.

4.5.3. Vegetal matter in wolves' diet

Fruit and seeds occurred often in scats (19%) and represented 3% of the REB. The remains of fruits found (apple, rowan, watermelon, plum, hazelnut) as well as the seeds of *Heracleum sp.*, *Myrrhis sp., and Ranunculaceae* suggest that the consumption of fruits is intentional and may serve as an additional source of vitamins and minerals (Mech 1970, Castroviejo 1975, Andersone & Ozolins 2004). Many studies, especially in Spain and Italy (Guitian *et al*. 1979, Cuesta *et al*. 1991, Meriggi *et al*. 1996) showed a frequent consumption of those and other fruits. Some studies also mentioned an interesting difference in adult and pup diet. Van Ballenberghe *et al*. (1975) and Fritts *et al*. (1981) reported a high incidence of berries in scats collected at rendezvous sites. It suggests that berries are primarily eaten by pups. At rendezvous site, the pups waiting for the adults back with food may look around and find fruits to eat, an appreciable amount of food and vitamins. From our observation in the field (Becker *et al*. 2010), young wolves clearly ate fruits intentionally and in such amount which suggest that fruits are food items despite their low nutritional value.

Other plant items (leaves, stems, wood, buds) might have been ingested by chance while wolves were feeding on the ground (Müller 2006). However, as we found them in 87% of scats, we would suggest that some were intentionally ingested. Leaves often appeared folded and sometimes there were entire leaves, which may fill a purgative role (Huffman 1997, 2001, Krief 2004). These authors found in several species of great apes that folded or even entire leaves were ingested and found intact in faeces and had a purgative and medicinal role. Leaves act as a mechanical vermifuge, irritating the intestinal lining and promoting the expulsion of parasites (Wrangham 1995, Huffman 1997, 2001, Krief 2004). Spruce needles and leaves of ericaceous plants were considered to be ingested with prey by Kuyt (1969), as they constitute the biotope where wolves are hunting. As we observed wolf pups eating bog moss, pine buds and birch bark, we will considered them as intentionally consumed although their function remains unknown. Self-medication (Ansay 2002) could be a valuable hypothesis but needs to be investigated in the future.

We also observed a high occurrence of grass (Graminae) (68% of scats), which is in accordance with wolf diet studies all over the world (Kuyt 1969, Gade-Jorgensen & Stagegaard 2000, Tremblay *et al*. 2001, Capitani *et al*. 2004). This may be due to the higher availability of plant material in summer. Grass consumption is supposed to be useful as a purgative to eliminate intestinal parasites and aid in cleaning the intestine of hair (Mech 1970, Peterson & Ciucci 2003).

4.5.4 Methods comparison

Wolf scats could be confused with those of dogs or foxes, but application of the mentioned criteria of faeces characteristics in hesitant cases ruled both of these out. Even though some faeces could eventually belong to wild dispersers, we consider the number negligible (Kohira & Rexstad 1997). Moreover, the wild dispersers could have been the released wolves from previous years so in that regard, part of the same study. In addition, no wild pack faeces could have been collected due to the absence of established populations of wild wolves in the release area.

Carnivores' diet studies, and faecal analysis in particular, often suffer from difficulties in estimating the proportions of the true biomass consumed (Ansorge 2006). Here we used and compared 4 methods of diet estimation, including the Weaver's (1993) method of biomass calculation. Correlation coefficients resulting from the pairwise comparisons demonstrated that the analysis methods ranked food items quite similarly. We nevertheless observed some differences in those rankings between REB, biomass and percentage of occurrence methods. Biomass model is likely to assigned higher ranks to large mammals (i.e. ungulates, sheep, etc.) and lower ranks to small animals (i.e. insects, micro-mammals, wild birds, etc.) than the other methods do (Ciucci *et al*. 1996). Some sources of difference between methods might be due to the quantification process. The percentage of occurrence method accounted for the presence of an item whereas the two other methods (REB and biomass) also take into account the amount of the item in the scat sample (Ciucci *et al*. 1996). Thus the quantity of small animals consumed may be overrepresented by percentage of occurrence method compared with larger animals (Mech 1970, Floyd *et al*. 1978, Huitu 2000). Percentage of occurrence method takes into account prey items contributing various amounts by volume to a scat equally and not in their respective proportions (Huitu 2000). The latter as well as REB method undergo biases due to changes in surface/volume proportion in prey of different sizes (Ciucci *et al*. 1996). Wild ungulates biomass might be overestimated if wolves have only eaten small pieces of the animal or carcasses remains from hunters instead of the entire animal. It is known that wolves often do not consume prey entirely in a single meal (Miller *et al*. 1985, Ciucci *et al*. 1996). Moreover, the live weight of prey might not reflect the reality as they were species not adjusted weights calculated from proportions of juveniles, adults, females and males actually eaten (Corbett 1989). The biomass model took in consideration neither the part taken from scavengers nor the possible poor physical condition of the prey (Ciucci *et al*. 1996). Wild ungulates proportions might be underestimated by the REB method compared to the REB of other wild mammals because of difference in digestibility of prey types (Lockie 1959, Weaver & Hoffman 1979). Large prey may be higher digestible than smaller ones, for which entire prey is ingested with all hair and bones then recovered more easily in scats. The way in which the wolf eats its prey may certainly be a source of bias as well as the order in which the prey are eaten (Lockie 1959). Individual wolf may meet differential digestibility, especially of bone remains (Kelly 1991). For instance, the digestive system of young wolves is less efficient compared to the one of adults (Reynolds & Aebischer 1991).

Finally, it is relevant to stress that methods differ in sort: all methods except biomass model, measures undigested food remains in scats whereas biomass estimates relative importance of food items in terms of actual live prey ingested (Ciucci *et al*. 1996). The great differences between rankings by REB or biomass and percentage of occurrences involve particularly food items (small animals, fruit and seeds) whose remains were structurally diverse and weigh not as much of large mammal remains (Ciucci *et al*. 1996). Thus, interpretation of statistical comparisons of the different rankings should be careful. This considered, we might however highlight that differences among rankings for particular food items did not significantly influence the overall assessment of the diet. Indeed, the relative importance of the main food types (i.e. wild ungulates, middle-sized mammals, domestic animals, etc.) was revealed by all methods. Ciucci *et al*. (1996) as well as Spaulding *et al*. (1997) found similar results.

4.6. References

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Chapter 5. Evaluation of the performance of two GPS telemetry collars for wolf monitoring in the boreal forest

Chapitre 5. Evaluation de la performance de deux colliers GPS pour le suivi de loups en forêt boreal

Глава 5. Оценка работы двух GPS ошейников для мониторинга волков в тайге

5.1. Abstract

Abstract: We compared the performance of two models of GPS collars, with different way of data transmission, the GPS/GSM collar Lotek WildCell 4400S and the GPS/Argos collar ES-PAS Pulsar. We assessed the influence of vegetation and topography characteristics, movement and speed, and behaviour or position of head of collared wolf on the success rate of fixes acquisition of GPS collars. We tested the collars in 4 environment types (open area, young forest, old forest, and valley), at 3 speeds (0, 5 and 12 km/h) alone and fitted on dog, and on captive wolf. We found significantly different success rates in habitat, with about 90-100% successful attempts in open areas, 40-70% under canopy and 15-70% in valleys. The speed did not seem to influence the success rates but affected the time in fix acquisition. Wolf movement had little impact on collar performance, but wolf head position decreases the success rates when animal was bedding, head beside. Overall performance was greater for the Lotek model, but this one was not usable in Russian remote boreal forest where GSM coverage is poor or null. ES-PAS model did not fail in data transmission and was better designed for wolf neck.

Key words: Global Positioning System, Argos, location success, satellite telemetry, *Canis lupus*, canopy closure, behaviour.

Résumé : Nous avons comparé la performance de deux modèles de colliers GPS, avec différent moyen de transmission des données, le collier GPS/GSM Lotek WildCell 4400S et le collier GPS/Argos ES-PAS Pulsar. Nous avons évalué l'influence de la végétation et de la topographie, du mouvement et de la vitesse, et du comportement et de la position de la tête d'un loup équipé sur le taux de succès d'acquisition des points des colliers GPS. Nous avons testé les colliers dans 4 milieux (zone ouverte, forêt jeune, forêt âgée, zone encaissée), à 3 vitesses (0, 5 et 12 km/h) seuls et sur un chien, et sur un loup captif. Nous avons trouvé des taux de succès significativement différents selon les milieux, avec environ 90% d'essais réussis en zone ouverte, 40-70% sous canopée, et 15-70% en zone encaissée. La vitesse ne semble pas avoir d'influence sur le taux de succès, mais affecte le temps d'acquisition d'un point. Le mouvement du loup a peu d'impact sur la performance des colliers, mais la position de la tête du loup diminue le taux de succès lorsque l'animal dort la tête sur le côté. Dans l'ensemble, la performance était meilleure pour le modèle Lotek, mais celui-ci s'avère peu utilisable en forêt boréale russe où la couverture GSM est pauvre, voire nulle. Le modèle ES-PAS n'a pas montré d'échec dans la transmission des données et était mieux adapté au cou du loup.
Mots-clés : Global Positioning System, Argos, succès des localisations, satellite télémétrie satellitaire, *Canis lupus*, couverture forestière, comportement.

Абстракт:

Мы сравнили работу двух моделей GPS ошейников, с различным способом передачи данных, ошейник GPS/GSM Lotek WildCell 4400S и ошейник GPS/Argos ЕС-ПАС Пульсар. Мы оценили влияние растительности и топографию, движение и скорость, поведение и положение головы волка, для уровня успешных попыток получения локацией GPS ошейников. Мы проверили ошейники в 4 типах окружающей среды (открытая зона, молодой лес, старый лес, и долина), на 3 скоростях (0, 5 и 12 км/ч) без животного и на собаке, и на волке в неволе. Мы нашли достоверно различные доли успешных попыток в среде, с приблизительно 90 % удачных попыток в открытой зоне, 40-70 % под сенью и 15-70 % в долинах. Скорость, казалось, не влияла на доли успешных попыток, но затрагивала время получения локацией. Движение волка оказало небольшое влияние на работу ошейников, но положение головы волка уменьшает количество успешных попыток, когда животное спит с повернутой головой на сторону. Эффективность работы была больше для модели Lotek, но этот ошейник не был удобный для использования в русской тайге, где телефонная сеть низкая, или отсутствует. Модель ES-ПАС не показала провал в передаче данных и была лучше приспособлена для волка.

Ключевые слова: Система глобального позиционирования, Argos, успех локализаций, спутниковая телеметрия, *Canis lupus*, лесное покров, поведение.

5.2. Introduction

Telemetry allowed great progress in the research on wildlife, with the possibility to locate the animal at any time (Mech & Barber 2002). Even for common and well-studied species, the technological advances allowed to better understand the life of animals in their ecosystem. Wolf (*Canis lupus*) monitoring by telemetry was first realized at the end of the 1960s in Ontario, Canada (Kolenosky & Johnston 1967). But soon, the VHF (very high frequency) telemetry showed its limits and constraints for animals that occupy remote areas or that have extensive movement patterns. In those case, satellite telemetry has many advantages (Ballard *et al*. 1995), and the technological progresses in transmitter miniaturization have made possible placing satellite collars on mid-sized mammals such as wolves since the 1990s (Ballard *et al*. 1995, Merril *et al*. 1998).

Satellite telemetry has been primarily used with transmitting collars (Buechner et al. 1971) rather than receiving collars (Rodgers et al. 1996). Transmitting collars transmit to satellites which transfer the data to earth. Receiving collars calculate and store positions with data from an internal Global Positioning System (GPS) that scans 24 earth-orbiting satellites. The satellites continuously broadcast radio signals and a GPS receiver must simultaneously receive signals from ≥ 3 such satellites to determine its 2-dimensional position (latitude, longitude), better ≥ 4 satellites for its 3-dimensional position (*idem* plus altitude) (Merrill *et al*. 1998). GPS collars are about 10 times more expensive than conventional VHF collars, but the latter require manual data collection that is time and money consuming. GPS collars can localize an animal frequently during day or night regardless of weather (Rodgers *et al*. 1996, Edenius 1997). Relative to other techniques, GPS collars have the potential for gathering greater amounts of data, with greater safety for the researcher (Johnson *et al*. 2002) and without the temporal biases associated with weather and daylight (Springer 1979, Beyer & Haufler 1994).

Most studies on collared wolves have been realized in North America, but also in Spain (Vila *et al.* 1995), in Byelorussia and Poland (Jedrzejewski *et al.* 2002 ; Theuerkauf *et al.* 2003), in Scandinavia (Alfredeen 2006 ; Kojola *et al.* 2006), in Slovakia (Findo & Chovankova 2004), in India (Jethva & Jhala 2004), and more recently in France in the frame of a research program on the impact of wolves on wild ungulates in the Alpes (Bernard-Laurent 2005). However, in Russia, huge wooded territory, no study has been made on satellite-collared wolves, apart from those in this PhD thesis (see Chapter. 3). Satellite monitoring is indispensable to the study and protection of the very diverse and disseminated fauna in Russia. But the vegetation, the relief and the rubbing of animals make it difficult with traditional collars (Salman 2010).

Manufacturers and the published literature have shown some limitations of GPS collars. Experimental trials have documented that terrain and canopy coverage can reduce the likelihood of a GPS collar acquiring the signals from 3 or more satellites necessary to calculate a position. In Ontario, Rempel *et al*. (1995) working in early spring in an experimental plantation dominated by coniferous tree species, concluded that location success was related positively to tree spacing and inversely to canopy closure. Rempel & Rodgers (1997) suggested that tree height was the most important variable influencing location success of GPS collars. Edenius (1997) concluded that location success was related inversely to canopy cover in Swedish boreal forest. Finally Dussault *et al*. (1999), testing collars in eastern Canadian boreal forest, found that number of satellites tracked by GPS receiver was related negatively to tree height. But as emphasized by Moen *et al*. (1996), more studies are needed under different types of forest and relief before results can be extrapolated to other sites.

D'Eon (2003) found that models including satellite availability, terrain and vegetation characteristics do not account for most missing data and suggested that animal behaviour is a large source of unexplained data loss from free-ranging animals. But few published studies have directly assessed behavioural influences on fix success. Only moose (Moen *et al*. 1996), white-tailed deer (Bowman *et al*. 2000) and brown bears (Graves & Waller 2006) have been observed during fix attempts. Both ungulate species had reduced fix success when animals were bedded. And in their models, Graves & Waller (2006) found that physical and movement characteristics of animals were the primary influences on fix success.

Most prior studies were conducted in boreal forest, but no one was conducted in vegetative communities of Russian Federation. Also, few previous studies have tested collars from different manufacturers simultaneously under identical conditions (Di Orio *et al*. 2003). Additionally, we had the opportunity to observe behaviour of a tame wolf female in naturally woody enclosure. Our objectives were to determine whether: 1) vegetation and topography characteristics, 2) movement and speed, and 3) behaviour or position of head of collared animal affected the success rate of fixes acquisition of GPS collars. We also compared the performance of the 2 models in those situations.

5.3. Material and methods

5.3.1. Study area

The study took place at the Biological Station “Chisty Les” (56°44’N, 31°31’E) situated 450 km north-west from Moscow, in the district of Toropets (3373 km^2), in the region of Tver, west part of Russian Federation. The area is situated at the southern limit of the boreal forest, called taiga. 80% of the territory is covered by forest composed of pine *(Pinus sylvestris)* and spruce *(Picea abies)*, together with birch *(Betula pendula),* aspen *(Populus tremula)*, and alder *(Alnus incana).* About 40% of the forest is primary, 60% is recovering the territory after the exodus of the local population since the collapse of the Soviet Union in 1990. The few opened areas are swamps and peats, abandoned fields and villages. Elevation is maximum 250 m with many hills. Rivers and streams flow in narrow valleys with rather steep slopes. The climate is continental with two main seasons, winter and summer. Temperatures vary between -40°C and +40°C. Permanent snow cover is present from November to April, with one meter depth average. Annual precipitations are important with 550-750 mm.

5.3.2. Description of the equipment tested

-GPS/GSM collar Lotek WildCell 4400S (Newmarket, Ontario, Canada)

The GPS system is based on the reception capacity of the collar that is to say its capacity to scan the 24 GPS satellites in orbit around the Earth. The receiver has an internal computer that saves the locations (Mech & Barber 2002). GPS satellites permanently emit radio signals and the receiver on the collar must receive those of minimum 4 satellites simultaneously so as to determine its position in 2 or 3 dimensions (2D or 3D, latitude, longitude, altitude) (Merril *et al.* 1998, Di Orio *et al.* 2003). The exact position is calculated thanks to the measure of the delay in the propagation of the signal, and thus the distance between the receiver and the satellite. To determine its position, the receiver must have an up-to-date almanac, an estimate of its own position and the current time of the day (Rodgers *et al.* 1996). With the ephemerid, the receiver can calculate its accurate position resolving a system of 4 equations with 4 unknown data: latitude, longitude, altitude and time satellite/receiver. There are several options for the user to remotely get the positions saved in the collar. In our case, the collar has a GSM (Global System for Mobile Communication) option, which works similarly to a mobile phone. The collar has a SIM (Subscriber Identity Modulecard that allows reception and emission of messages. The collar determines its positions and sends them by SMS (Short Message System) to a modem that has a SIM card too (Bourgeois 2009). If the animal is out of good GSM coverage, the data are saved and sending attempts will be done later (Walzer & Kaczensky 2008). There is thus a 2-way communication, to the collar and from the collar, which makes possible a remote programming. The collar is provided with a drop-off system which releases the collar after a pre-programmed period and allows its recover at the end of the study and limits the impact on the animal over the time. In this case, positions are also available by connecting directly the collar to the computer. Finally the collar has a VHF option which allows the localization of the animal in case of failure in the GPS system (Fig 5.1).

-GPS/Argos collar ES-PAS Pulsar (Moscow, Russian Federation)

The telemetry system Argos came out from the cooperation between the Centre d'Etudes Spatiales (CNES, France), the National Aeronautics and Space Administration (NASA, USA) and the National Oceanic and Atmospheric Administration (NOAA, USA) (Mech & Barber 2002). It has become the main way of monitoring marine or terrestrial vertebrates' species over long distances (Witt *et al.* 2010). Each platform has a unique identification number and sends a signal every 90 to 200 seconds with a pulsation of about 1/3 second (Mech & Barber 2002, Collecte Localisation Satellite 2008). The satellites situated on low polar orbit are numerous enough to ensure a global coverage. They can receive the signal of any platform in a diameter of 5000 km (Taillade 1992, Collecte Localisation Satellite 2008). When the satellite passes over the animal, there is a window of 10-12 minutes during which a signal emitted by the platform can be received. The platform localization is based on the Doppler-Fizeau effect, which is when the signals received by the satellite during its pass over the platform will have different frequencies, because the satellite is moving. The platform continuously emits a signal at a certain frequency, here 401,650 MHz. Platforms must be powerful enough to send signals to the satellites, 800 to 4000 km away; the power of emission should be between 250 mW and 1W (Howey 1992, Taillade 1992). When an Argos satellite receives a signal from the platform, it records the frequency and date, reported on magnetic bands and transmitted to a reception station when the satellite passes over it. The station sends the data to a treatment centre that forward them to the researchers. With the present collars, the Argos system was combined with a GPS device, which works as described above. The GPS receiver determines the new position with regular intervals and high precision. Both GPS and Argos locations are sent at the time of the emission by the Argos beacon (every one or three emissions depending on the collar programmation). The transfer of date via Argos involves an additional cost, but is rather to function even in remote areas (Fig 5.2).

Fig 5.1: Functional process of the GPS/GSM collar Lotek WildCell 4400S (adapted from Collection Localisation Satellite 2008).

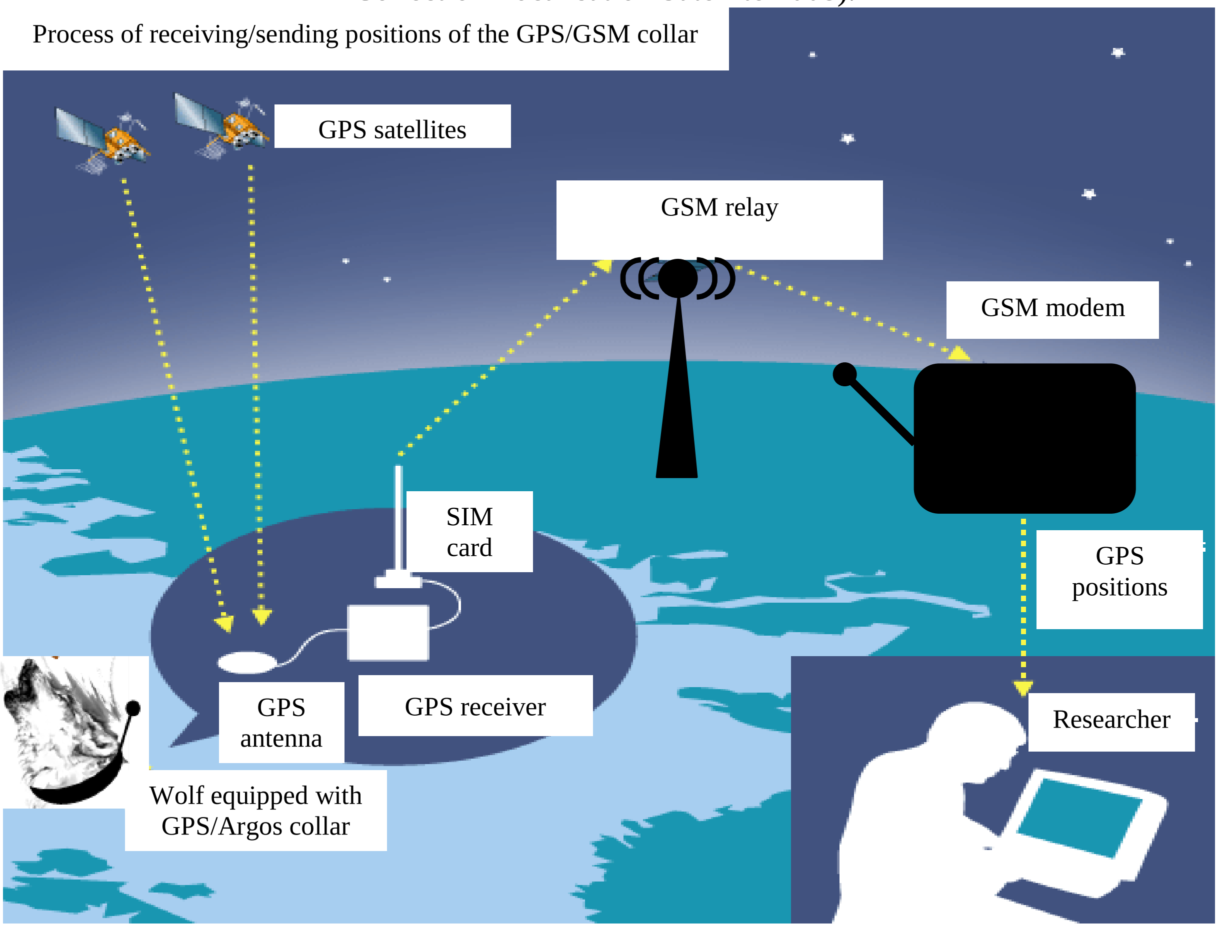
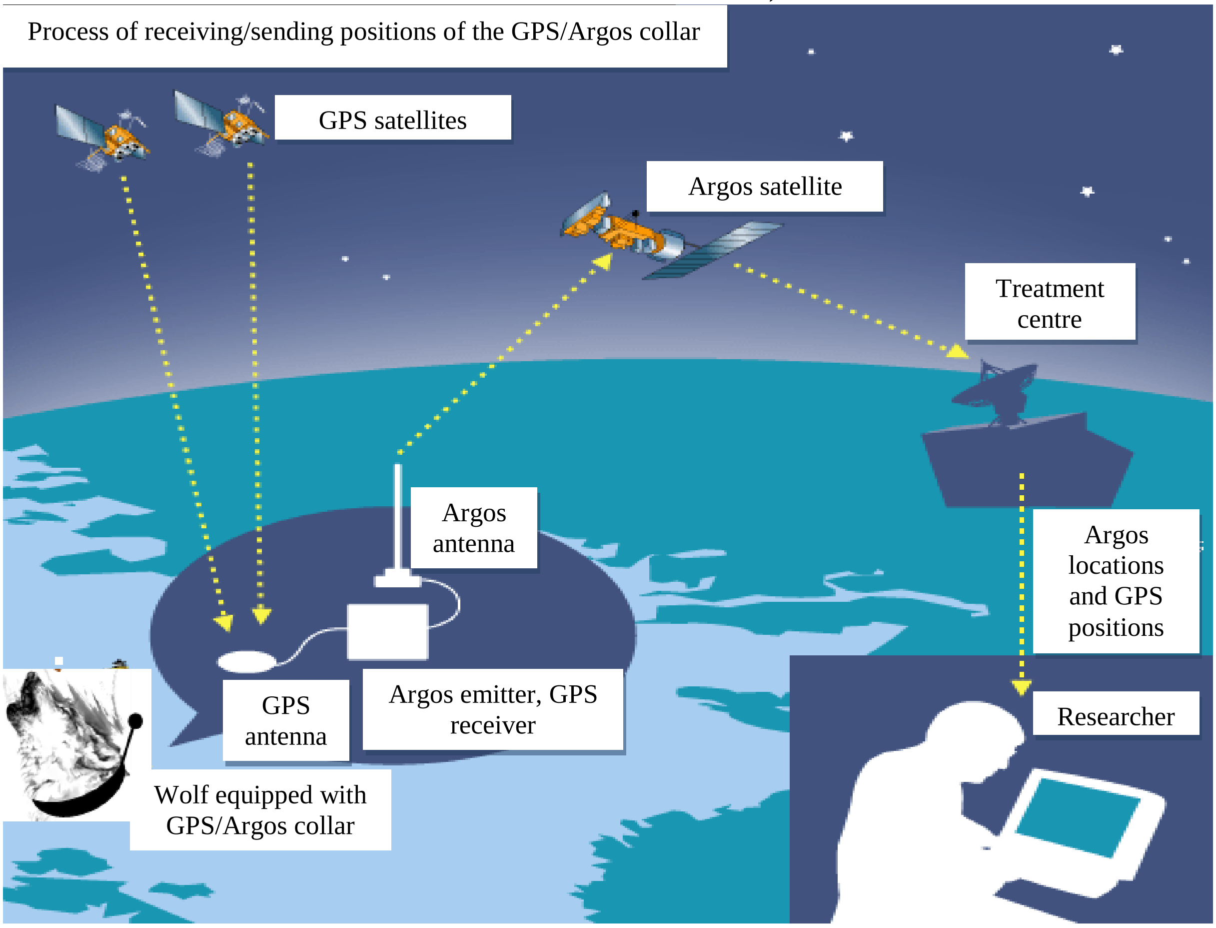


Fig 5.2: Functional process of the GPS/Argos collar ES-PAS Pulsar (adapted from Collection Localisation Satellite 2008).



We compare the characteristics of both collars in Table 5.1.

Table 5.1: Characteristics of GPS/GSM collar Lotek WildCell 4400S and GPS/Argos collar ES-PAS Pulsar, concerning technical specificities, user's easiness and animal welfare.

	GPS/GSM collar Lotek WildCell 4400S	**GPS/Argos collar ES-PAS Pulsar**
PHOTO		
TECHNICAL SPECIFICITIES		
Content	GPS receiver VHF beacon Computer/memory module	GPS receiver Argos beacon Computer module
Operational life	1 year (6 fixes per day)	1 year (4 hours ON / 4 hours OFF)
Operating temperature	-30˚C to +50˚C	-35°C to +50°C

USER'S EASINESS		
Programming	Remotely changeable at any time, provided collar is under GSM coverage	Unchangeable
Data collection	GSM modem (needs coverage), or directly from the collar	Internet via Telnet (ArgosServer.cls.fr)
Ease of use	Sent in pieces with general manual	Pre-programmed, ready to use
Purchase price	1810€ (collar) + 935€ (download link) + 400€ (GSM modem)	2150€ (collar) + 105€/month (Argos data transmission)
After-sale service	Long delay, basic answers	Effective and reactive, by e-mail, phone and on the place
ANIMAL WELFARE		
Size	Dimensions: 260x50 mm (HxL) Collar size: 44-50 cm	Dimensions: 205x50 mm (HxL) Collar size: 37-42 cm
Weight	690g	650g
Drop-off	Yes	No
Material	Rigid, hard to handle	Flexible, easy to handle
Design	Oval-shaped, unbalanced distribution of the components	Round-shaped, balanced distribution of the components

5.3.3. Data collected

We performed 3 series of tests so as to assess the influence of 1) the environment, 2) the movement, and 3) the wolf behaviour on the performance of GPS collars.

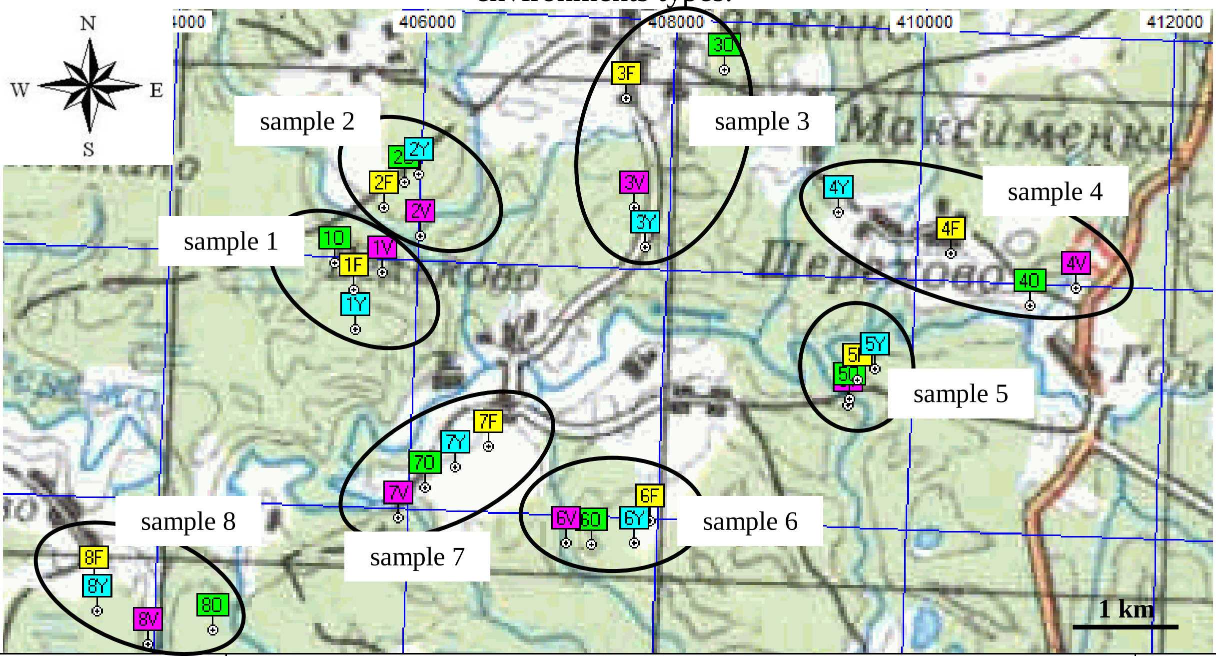
-Influence of the environment

We defined 4 types of environment: open area / young forest / old forest / valley and localized 8 sectors with all 4 types (Fig. 5.3).

Both collars were placed simultaneously in a site, for one hour, at about 70 cm from the ground, on stick. The GPS/GSM collar Lotek WildCell 4400S is scheduled to determine a fix every 5 minutes. The GPS/Argos collar ES-PAS Pulsar is programmed to define a position every 210s ±10% (and Argos data emission every 70s ±10%).

Data are collected after the tests directly to the collar or by GSM modem for the GPS/GSM collar Lotek WildCell 4400S, and by connection to Telnet for the GPS/Argos collar ES-PAS Pulsar. We sum up the positions received for each environment types (8 samples of 1 hour, each). Data were collected in May 2010.

Fig. 5.3: Position of the 8 sampling sectors in the study area and definition of the environments types.



Environment type	Definition	Code
Open area	Field, glade, village, road, etc. Place with >80% sky opening.	#F
Young forest	Forest less than 40 years old, mainly composed of deciduous species, low trees, high density stem, low canopy closure, 40-80% sky opening.	#Y
Old forest	Forest more than 40 years old, mainly composed of coniferous species, high trees, low density stem, high canopy closure, 0-40% sky opening.	#O
Valley	Bottom of valley usually made by stream, moderate lateral obstruction.	#V

-Influence of the movement

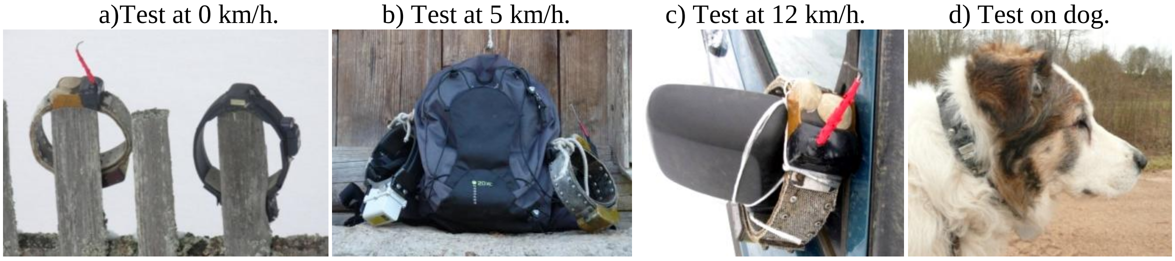
The aim of the tests is to understand the impact of speed on the ability of the collars to determine and send their positions. Collars were tested at speed of 0 km/h, 5 km/h and 12 km/h, in two situations: collar alone or collars fitted on a dog (*Canis familiaris*). Speeds of 5 and 12 km/h should represent respectively the pace and trot allures of wolves. The tests on dog are made to reproduce the influence of the animal and its fur. So as to minimize the influence of the environment on these tests, they were made in open areas (fields and open roads). At 0 km/h, collars were placed in a field on sticks at 70 cm from the ground, or fitted on a dog immobile in a field. At 5 km/h, collars were attached on both sides of a back pack while a person walked, or fitted on a dog walking at the lead. At 12 km/h, collars were attached on both sides of a car while driving, or fitted on a dog running at the lead. The GPS/GSM collar Lotek WildCell 4400S is scheduled to determine a fix every 3.5 minutes. The GPS/Argos collar ES-PAS Pulsar is programmed to define a position every 210s ±10% (and Argos data emission every 70s ±10%).

Data are collected after the tests directly to the collar or by GSM modem for the GPS/GSM collar Lotek WildCell 4400S, and by connection to Telnet for the GPS/Argos collar ES-PAS

Pulsar. We sum up the positions received for each situation combining the speed and the presence/absence of dog. Tests were conducted in March-May 2011. (Fig 5.4).

Fig 5.4: Illustrations of the test regarding the influence of movement:

a)Test at 0 km/h. b) Test at 5 km/h. c) Test at 12 km/h. d) Test on dog.



-Influence of the wolf behaviour

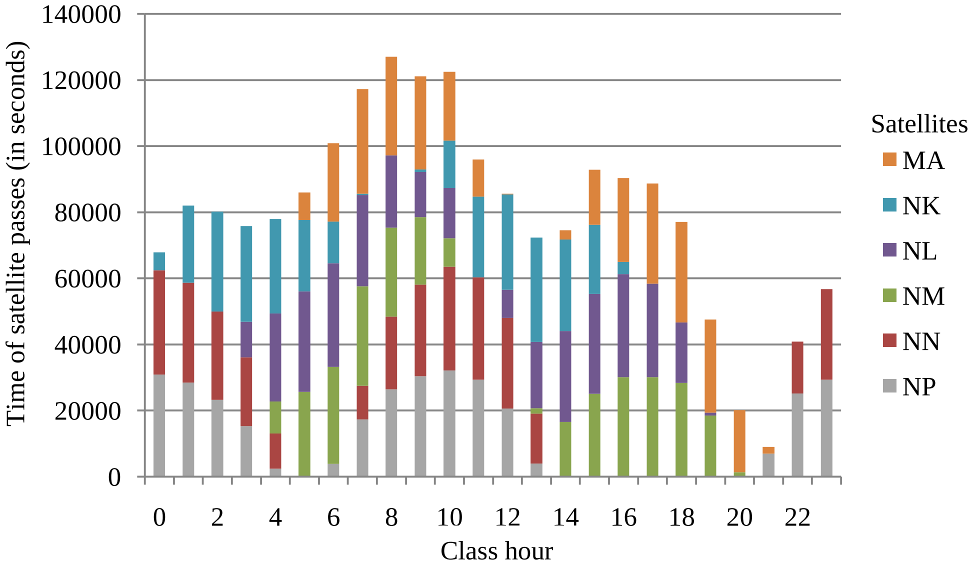
In order to assess the influence of wolf behaviour on the performance of GPS collars, we equipped a 4 year-old tame wolf female alternatively with the GPS/GSM collar Lotek WildCell 4400S, and the GPS/Argos collar ES-PAS Pulsar. We reported the behaviour of wolf classified in position of the head (up/bottom/beside) and the mobility of the wolf (mobile/immobile). We used the focal method with an ethogram (Table 5.2).

Table 5.2: Ethogram used for the test on the influence of wolf behaviour on the performance of GPS collars.

Behaviour	Code	Description
Head up	HU	The wolf's head is up, away from the ground.
Head bottom	HB	The wolf's head is down on the ground or close to it, ears up.
Head beside	HS	The wolf's head is down on the ground, one ear on the ground.
Immobile	IM	The wolf is not moving, but is standing, sitting or lying.
Mobile	MO	The wolf is moving, walking, running or jumping.

To maximize the chance of getting fixes, we realized the observations at hours when the passes of satellites were more frequent. According to the Argos predictions (Fig. 5.5), this was between 7h and 10h, GMT time. The predictions gave the window of time when a satellite will be over the platform. The GPS/Argos collar ES-PAS Pulsar was programmed to define a position every 90s ±10% (and Argos data emission every 90s ±10%). The GPS/GSM collar Lotek WildCell 4400S was scheduled between 7h and 10h, GMT time to determine a fix every 5 minutes. The focal sessions were realised at time of satellite passes for the GPS/Argos collar and at time when the collar switches ON and for 180s long for the GPS/GSM collar. The changes in position of head and mobility of the wolf are reported.

Fig 5.5: Time of passes of Argos satellites per class hour during the study period, 31/01/2011-08/04/2011 (Argos predictions).



Data are collected after the tests directly to the collar or by GSM modem for the GPS/GSM collar Lotek WildCell 4400S, and by connection to Telnet for the GPS/Argos collar ES-PAS Pulsar. We sum up the positions received for behaviour, combining the mobility/immobility and the position of the head (HU/HB/HS). Tests were conducted in January-March 2011.

-Statistical analysis

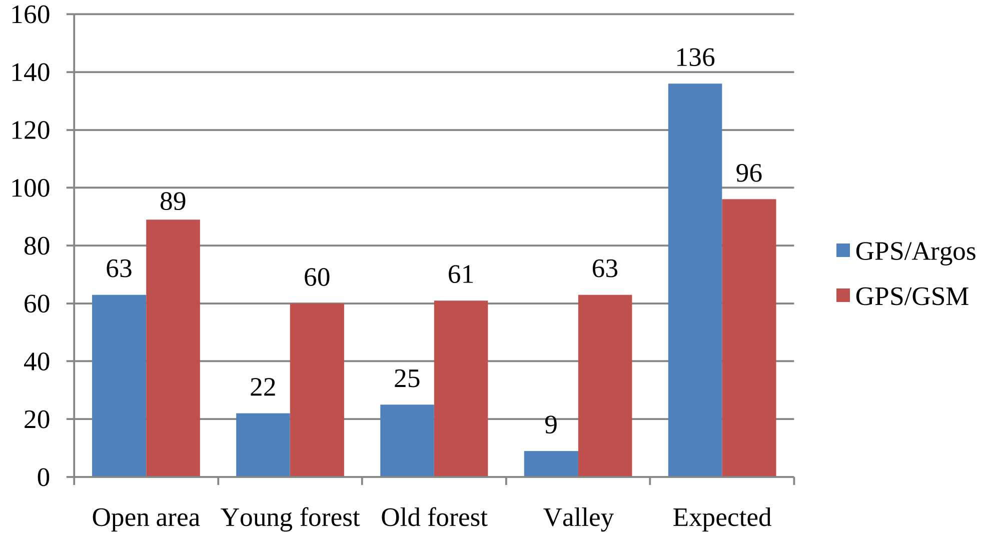
To test the influence of the environment, we proceeded to a G-test to see the difference of performance in the different environment types. We conducted a Generalized Linear Model (GLM) in R, using a method comparable to the one of Zuur *et al*. (2009). To test the influence of the movement, we proceeded to Student's tests to compare the performance in different situations. To test the influence of the wolf behaviour, we proceeded to a Chi-square test to compare the performance regarding the wolf head positions. Statistical analysis was performed with the software XLSTAT 2011.

5.4. Results

5.4.1. The influence of the environment

Both GPS/GSM collar Lotek WildCell 4400S and GPS/Argos collar ES-PAS Pulsar were tested in 4 different environment types, for 8 hours in each type. We collected 273 positions for the GPS/GSM collar and 119 positions for the GPS/Argos collar, with many variations between the types (Fig 5.6).

Fig 5.6: Number of positions received for the GPS/Argos collar ES-PAS Pulsar and the GPS/GSM collar Lotek WildCell 4400S in 4 different environment types.



We performed a G-test on both collars' results to see if there was a difference of performance depending on the environment types (Table 5.3).

Table 5.3: Statistic results of the influence of environment on the performance of GPS collars.

GPS/Argos collar ES-PAS Pulsar			**GPS/GSM collar Lotek WildCell 4400S**		
Log likelihood ratio statistic (G) = 51.0413, X-squared df = 3, p-value = 4.794e-11			Log likelihood ratio statistic (G) = 8.0053, X-squared df = 3, p-value = 0.0459		
Environment type	p-value	Holm	Environment type	p-value	Holm
1 Open area	0.000000000	0.000000	1 Open area	0.004863708	0.019455
2 Young forest	0.089926962	0.179854	2 Young forest	0.242139272	0.726418
3 Old forest	0.305330592	0.305331	3 Old forest	0.304885498	0.726418
4 Valley	0.000000756	0.000002	4 Valley	0.459095817	0.726418

According to the statistic results, the performance is significantly different in the environment types, both for the GPS/Argos collar ($p<0.01$) and for the GPS/GSM collar ($p<0.01$). The environment types responsible for the reject of the null hypothesis (*i.e.* uniform repartition of the number of determined fixes) are the open area and the valley for the GPS/Argos collar. There is obviously a too low number of fixes in the valleys and a too high number in open areas (respectively N=9 and N=63) in comparison with the fixes in young and old forest (respectively N=22 and N=25). For the GPS/GSM collar the open area is responsible for the reject of the null hypothesis. In the open areas, the number of fixes is higher (N=89) than in other environment types (N=60, N=61, N=63 respectively in young forest, old forest and valley).

Thanks to a GLM, we tried to explain the percentage of success in function of the collar model and the environment type (Table 5.4). The success was defined as the number of fixes determined in the field over the expected number of fixes if all the attempts had been successful. For the GPS/GSM collar Lotek WildCell 4400S scheduled for a fix every 5 minutes, we expected 12 fixes/hour. For the GPS/Argos collar ES-PAS Pulsar programmed for a fix every 210 seconds, we expected 17 fixes/hour. We are aware that in the latter case however, this number is far much overestimated because it does not take into account the passes of satellites, needed to send the data.

Table 5.4: Statistic results of the influence of environment and collar on the success.

	Df	Deviance	F value	Pr(F)
Collar model	1	405.16	100.168	2.492e-14 ***
Environment type	3	244.90	12.403	2.150e-06 ***

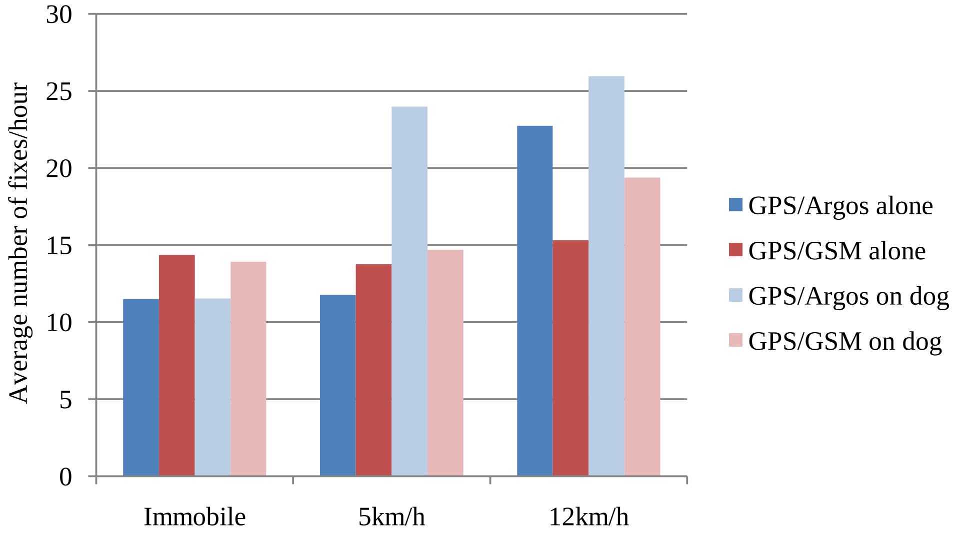
	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-1.8196	0.2908	-6.256	4.84e-08 ***
GSM collar	2.4677	0.2647	9.324	3.31e-13 ***
Old forest	0.1046	0.3505	0.299	0.766
Valley	-0.2684	0.3556	-0.755	0.453
Open area	1.7105	0.3591	4.764	1.28e-05 ***

Both collar model (GLM, F=100.168, p<0.01) and environment type (GLM, F=12.403, p<0.01) have an influence on the percentage of success. Looking at the estimated coefficients for this model, the positive one (2.4677) estimated for the GSM collar seems to indicate that the collar performs better. In total, whatever the environment type was, the GPS/GSM collar Lotek WildCell 4400S had an average success of 71.1%, with almost full success in open areas (92.7%) and two third of success in other types (62.5% in young forest, 63.5% in old forest, 65.6% in valleys). The GPS/Argos collar ES-PAS Pulsar had only 21.9% of success in total, with a high variation between the types: 6.6% in valleys, 16.2% in young forest, 18.4% in old forest, 46.3% in open areas.

5.4.2. The influence of the movement

Both GPS/GSM collar Lotek WildCell 4400S and GPS/Argos collar ES-PAS Pulsar were tested alone and on dog, at 3 speeds, 0, 5 and 12 km/h, for several hours. We calculated the average number of fixes per hour in each situation (Fig 5.7).

Fig 5.7: Performance of GPS/Argos collar ES-PAS Pulsar and GPS/GSM collar Lotek WildCell 4400S stationary and at speeds 5km/h and 12km/h, alone and fitted on dog.



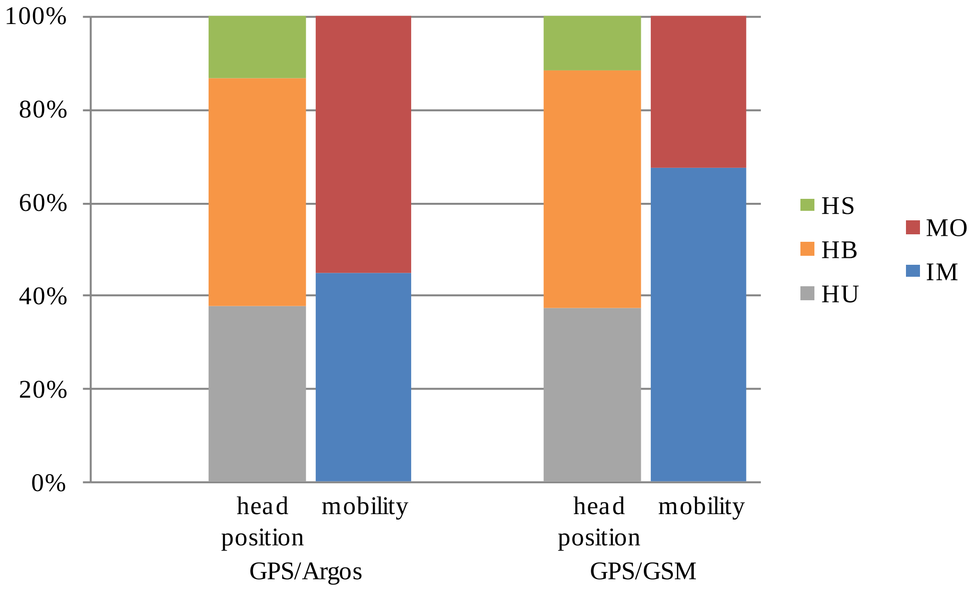
Both collars worked the best at 12 km/h on dog: 25.9 and 19.4 fixes/hour for the GPS/Argos collar ES-PAS Pulsar and the GPS/GSM collar Lotek WildCell 4400S respectively. The collars received in general more fixes when fitted on dog than alone, although differences were not significant (average for the GPS/Argos collar ES-PAS Pulsar, all speeds taken together, 20.5 fixes/hour on dog vs. 15.3 alone, $t=-0.885$, $p=0.428$; average for the GPS/GSM collar Lotek WildCell 4400S, all speeds taken together, 16.0 fixes/hour on dog vs. 14.5 alone, $t=-0.864$, $p=0.469$). Speed seems to have little effect on the acquisition, and collars had even better success at 12 km/h than 0 or 5 km/h in respective situations (average for both collars and situations taken together, 20.8 fixes/hour at 12 km/h vs. 12.8 and 16.0 at 0 and 5 km/h respectively). The GPS/Argos collar ES-PAS Pulsar overall performed better than the GPS/GSM collar Lotek WildCell 4400S (average for the GPS/Argos collar ES-PAS Pulsar, situations and speeds taken together 17.9 fixes/hour vs. 15.2 fixes/hour for the GPS/GSM collar Lotek WildCell 4400S, $t=0.897$, $p=0.405$).

5.4.3. The influence of the wolf behaviour

Both GPS/GSM collar Lotek WildCell 4400S and GPS/Argos collar ES-PAS Pulsar were fitted on captive wolf for several weeks and the wolf behaviour was observed while acquiring fixes. We collected a total of 111 and 89 fixes with the GPS/GSM collar Lotek WildCell

4400S and the GPS/Argos collar ES-PAS Pulsar respectively. We reported the position of the head and the mobility of wolf during acquisition (Fig 5.8).

Fig. 5.8: Proportion of fixes acquired in various situations of head position and mobility, and statistic results of Chi-square test.



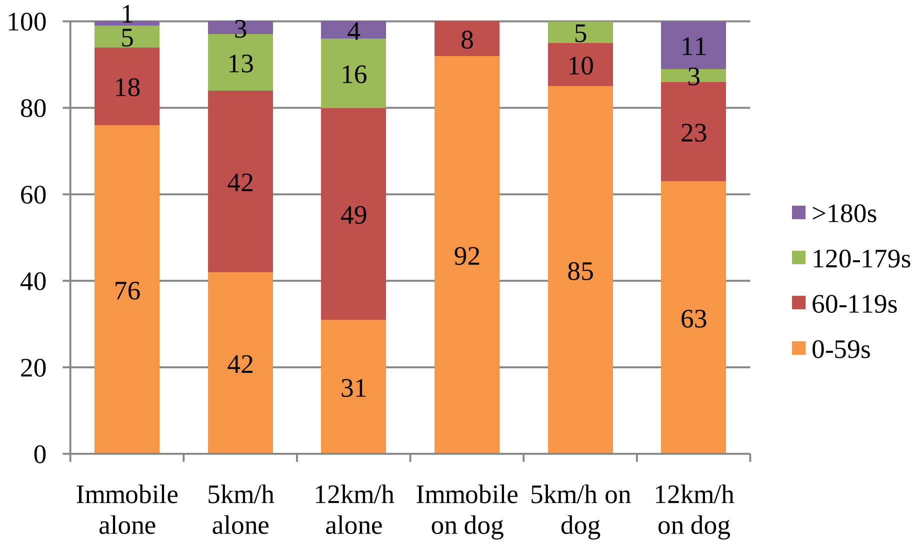
GPS/Argos head position	χ^2_1=0.19, p=0.000, **
GPS/Argos mobility	χ^2_1=0.01, p=0.314, ns
GPS/GSM head position	χ^2_1=0.24, p=0.000, **
GPS/GSM mobility	χ^2_1=0.12, p=0.000, **

Mobility of wolf seems to have little influence on the GPS/Argos collar ES-PAS Pulsar, as the fixes are equally obtained while wolf is moving and not moving (χ^2=0.01, p>0.05), whereas the fixes of the GPS/GSM collar Lotek WildCell 4400S are mostly obtained when the wolf is immobile (67.4% vs. 32.6%, χ^2=0.12, p<0.01). Regarding the position of the head, both collars had significantly different performances (GPS/Argos collar ES-PAS Pulsar: χ^2=0.19, p<0.01; GPS/GSM collar Lotek WildCell 4400S: χ^2=0.24, p<0.01). About half fixes are determined while the head is in bottom position, close to the ground for both collars (48.6% and 50.8% for GPS/Argos collar and GPS/GSM collar respectively). About 37% of fixes are obtained while the head is up (37.9% and 37.4% for GPS/Argos collar and GPS/GSM collar respectively). And the collars got less than 15% of fixes while the head was beside on the ground (13.5% and 11.8% for GPS/Argos collar and GPS/GSM collar respectively).

5.4.4. Accessibility to GPS and Argos satellites

We focused on the acquisition of fixes of the GPS/GSM collar Lotek WildCell 4400S and looked on the time needed to receive the signals of the necessary number of satellites. Satellites were found quicker when the collar was fitted on dog, and the speed had little impact on this time acquisition. Most fixes were determined in less than 1 minute when the dog was immobile, at 5 km/h or at 12 km/h (92%, 85% and 63% respectively). Few fixes were determined after 2 minutes, except at highest speed (14%). When the collar was immobile alone, it got most fixes in less than 1 minute (76%), but this performance decrease with speed. Less than half fixes were got within 1 minute (42% and 31% at 5 km/h and 12 km/h respectively), most were determined between 1 and 2 minutes (42% and 49% at 5 km/h and 12 km/h respectively), and many were still obtained after 2 minutes (16% and 20% at 5 km/h and 12 km/h respectively) (Fig 5.9).

Fig 5.9: Time needed for the GPS/GSM collar Lotek WildCell 4400S to acquire a fix in the different situations tested.



5.5. Discussion

5.5.1. General collars' performance

Our tests demonstrated the potential of GPS/Argos collar ES-PAS Pulsar and GPS/GSM collar Lotek WildCell 4400S for wolf research. Overall both collars performed well under most conditions. Success rates were more than acceptable for use on medium mammals with large home ranges. Higher success rates for Lotek collar could be attributed to improvements made by the manufacturer since previous studies (Di Orio *et al*. 2003), whereas the company ES-PAS is rather young and just started making collars for wildlife. Moreover, the ES-PAS model has been proved to perform better in natural conditions (*i.e.* on animal and in movement) than the Lotek model, which worked better on stationary situations.

The possibility of remote programming of the Lotek may be a useful tool in study with varying protocol, as well as to adapt the longevity of the collar to the study. In the mean time, the company ES-PAS may program the collar according to the customer's wishes, as the staff is very listening to the research needs and may adapt a collar to each situation. Release option of the Lotek is interesting both for animal welfare and cost saving. However, possible failure of the mechanism (Merrill *et al*. 1998) and difficulties in recovering the collar (Hebblewhite *et al*. 2007) may lead to expensive consequences. Hebblewhite *et al*. (2007) approximated the additional cost of animal capture to 25 500 €, which would be a huge unexpected financial burden in the budget of a study. With the Argos system of data transmission of the ES-PAS collar, there is no need to recover the collar at the end of the study. Also, the collar itself is manufactured in a quite cheap material and the loss of a collar would not be that important.

We did not experience failure collar failure during the tests but the collars were new and the study period short. However, we noticed important chewing damage on both collars when they were fitted on wolf. Novel object on a conspecific is often source of interest for other wolves and we saw the enclosure mates chewing the collar fitted on the tame female. The female itself could chew the Argos antenna of the ES-PAS collar. And risk of antenna cut that we experienced in other preliminary tests made us advice the company to improve the collar with internal antenna. Such new collar is already tested and gave good results (Salman 2010). Failure due to wolf chewing damage was already reported by Hebblewhite *et al*. (2007). In their study, they compare collar failures of various models deployed on different species in previous studies and found a similar overall performance measures between collars of 51% normal function, 16% failure, and 33% partial failure rates (Merrill *et al*. 1998, Johnson *et al*. 2002, Gau *et al*. 2004, Hebblewhite *et al.* 2007).

5.5.2. Impact of canopy and terrain

In accordance with previous studies (Moen *et al*. 1996, Edenius 1997), we found that under open sky 90-100% of attempts will result in GPS locations for the GPS/GSM collar Lotek WildCell 4400S. The estimation is more complicated for the GPS/Argos collar ES-PAS Pulsar, as number of fixes received also depends on the availability of Argos satellites. Our results were concordant with previous studies (Rempel *et al*. 1995, Edenius 1997, Rempel & Rodgers 1997, Dussault *et al*. 1999) demonstrating that fix rate declined under forest cover with about 10%-40% data loss. Under canopy closure, the percentage of successful location attempts decreases to 60% for the Lotek and to 30-40% (if compared to the successful attempts in open area) for the ES-PAS collar. We did not find difference of performance between the young high-stem-dense low canopy close forest and the old low-stem-dense high canopy close forest. We did not report the accuracy of positions, but De Cesare *et al.* (2005) found that high (>40%) canopy forests caused greater error than low (10-39%) and open (0-10%) canopy forests. Moen *et al.* (1996) explained the phenomenon in their study to stimulate the effect of canopy interference on location accuracy. While progressively reducing the number of available satellites, they conclude that reduced satellite availability is the cause for increased location error under canopy.

As D'Eon *et al*. (2002) and Frair *et al*. (2004), we found that topography impact on collar performance. In particular, fix rates decline in narrow valley bottoms, but the two models reacted differently. The Lotek collar showed only 40% of data loss in valleys, whereas the ES-PAS collar gave only 15% of fixes (compared to the successful attempts in open area). Again for the Argos system of data transmission, the availability of sky is a major factor influencing the success. Even if numerous satellites are above the horizon, if the animal is standing very close to a tree trunk, in a ravine, or under very dense canopy, the GPS unit may not have the required minimum of 3 satellites in view, and the Argos antenna may miss the satellite passes for data transmission (Rodgers *et al*. 1996, D'Eon & Delparte 2005).

5.5.3. Impact of animal movement and position

We did not find clear influence of the movement or speed on the collars' fix success, but the time of fix acquisition was clearly negatively affected by movement and speed when the collars were tested alone. Moen *et al*. (1996) recorded no effect of moose movement, whereas preliminary study of Edenius (1997) found that movement may negatively impact on collar performance.

The phenomenon to explain the loss of fixes on free-ranging animals comparing to stationary situations may not be the movement or speed, but the behaviour or the position of animal during a behaviour. Moen *et al*. (1996) found a 12% increase in failed fix attempts when GPS collars were moved from the vertical to the horizontal orientation, whereas Bowman *et al*. (2000) demonstrated no change in fix success based on collar orientation. But they demonstrated that fix success was affected by behaviour, especially when deer were bedding. They had less fix success, probably because their collars were close to the ground and thus more likely to be obstructed visually. Graves & Radandt (2004) found results to support this hypothesis as their collars had higher fix success when antennas were placed 66 cm above the ground versus 0-25 cm. Merrill *et al.* (1998) suggest that the antenna may point away from the sky when animal is sleeping and thus causes batteries to expend more power per attempt and eventually shortens GPS life. Graves & Waller (2006), working with bears, also thought that the direction of antenna may affect the fix acquisition. Animals could block satellite signals with their bodies, especially if they sleep with the antenna directed to one side. Bears sometimes push collars to the side when they bed, thus changing the position of the antenna relative to the horizon and decreasing the amount of available sky and the number of visible satellites. D'Eon & Delparte (2005) found support in this sense and have demonstrated that the angle of the collar relative to the sky or horizon is a large potential source of bias. In our study too, when wolf was sleeping or resting with the head on the side, the collars less performed. Surprisingly, collars got more fixes when the head was in bottom position than in up position. This might be because when the head was in bottom position, on the ground or close to the ground, the antenna must look to the sky; whereas when the head was in up position, the collars were spinning around wolf's neck and antenna may look to the side of bottom.

These results imply that the link between animal activity and collar positioning should be an important factor in collar performance and location accuracy. As D'Eon & Delparte (2005) showed reduced performance with lower collar angles relative to the sky or horizon, animal activities that place collar antennae at low angles (e.g. foraging, bedding, digging) will have higher bias than other activities that place collar antennae at higher angles (e.g. walking). More work on the link between animal movement and position and GPS performance is required to be able to make definitive recommendations for researchers.

The performance of GPS receiver to acquire a fix when the collar is fitted on a dog could suggest that the magnetism of animal fur influence the speed of acquisition. The antenna of the receiver has to intercept the electromagnetic energy propagating in the air before the receiver treated it (Kuechle 2005). It may thus be possible that dog hair creates a particular magnetic field around the animal, or that they play the role of antenna (Le Berre, personal communication). According to Salman (personal communication), the phenomenon is real but has never been studied and the static electricity of fur could be the cause, but other hypothesizes are possible and should be deeper investigated.

5.5.4. Implications for wolf monitoring

According to the overall performance of fix acquisition success, one would probably use the GPS/GSM collar Lotek WildCell 4400S to monitor wolf. However, during the field trials, we were often confronted to poor GSM coverage and did not receive the data by SMS as programmed. We were thus forced to link the collar at the computer after every test. In the field, it is unlikely to recapture free-ranging animals to get data from the collar. So in remote study areas of Russia, where GSM coverage is not guarantee everywhere, we would recommend the transfer of data by Argos system.
Regarding animal welfare, the GPS/Argos collar ES-PAS Pulsar is lighter than the Lotek model. Although other researchers have used collars weighing 1.08-1.22 kg on wolves (Ballard *et al*. 1995), the heavier the collar is, the greater chance that it affect the animal's movements and activity (Merrill *et al*. 1998). Also, the ES-PAS model was better designed and balanced for the neck of wolf (Fig 5.10). The drop-off option of the Lotek model is indubitably a plus for animal well-being, as it will not carry the collar more than the study lasts. But it could be easily added on the ES-PAS model in the future.

Fig 5.10: Photos of wolf wearing the GPS/Argos collar ES-PAS Pulsar (a) and the GPS/GSM collar Lotek WildCell 4400S (b).

a

b

We did not tested the accuracy of locations as this study was done in the frame of wolf reintroduction and we were more interested in general movement patterns and survival of wolves on the long-term than in habitat details. However, our results show again the high influence of terrain, canopy and animal behaviour on fix attempts success. As Bowman *et al*. (2000) highlighted, researchers should be concerned in the risk of underestimation the importance of a habitat. Indeed, if a behaviour or a habitat characteristic predisposes the animal to missed fixes, the researcher may underestimate this habitat.

Although potential biases, associated with relocation schedules being dictated by light and weather patterns in conventional VHF radio-telemetry programs, are reduced or eliminated with the use of GPS collars, biases related to blockage of signals by vegetation, topography and animal behaviour remain. Advances in GPS technology are likely to reduce but not eliminate this problem (Lindzey *et al*. 2001). However, many studies had now showed that GPS telemetry may be a very valuable tool in wildlife telemetry, as it provides high accuracy of locations and high percentage of successful location attempts (Edenius 1997). Until further refinements are made, both GPS collars we tested will be valuable to many researchers studying the movements of wolves, provided they choose the model the best adapted to their study design and study area. Wildlife professional must choose the too that best meets study objectives and budget (Johnson *et al*. 2002).

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Chapter 6. Habitat evaluation for grey wolves in Tver region, Russian Federation

Chapitre 6. Evaluation de l'habitat du loup gris dans la région de Tver, Fédération de Russie

Глава 3. Оценка среды обитания для серых волков в Тверской области, Российская Федерация

6.1. Abstract

Abstract: A number of important attributes must be considered when selecting sites for potential wolf reintroduction, including habitat type, prey abundance, human disturbance. The more optimal the conditions are at a reintroduction site, the higher the probability of successfully establishing a wolf population. Using the data of wolf census from the yearly Winter Route Survey of 2003-2005, we analysed the main habitat variables influencing the distribution of wolf *Canis lupus* in Tver region, Russian Federation. We looked for correlation using linear regression between 6 variables and the distribution of wolf in the 36 districts of Tver region. We found highest positive correlation with forest and low but negative correlation with human density: wolves were distributed in more woody and less populated districts. We then focused and 2 well-studied districts, Nelidovsky and Toropetsky districts, and looked for variables of human disturbance that maximize the differences between areas where the wolf is present and the ones where it is absent. Wolf plots were characterized by significantly lower density of villages and higher forest cover than wolf-free plots. Natural and artificial barriers such as river, roads and railways seem to have no influence on habitat suitability. We conclude in predicting suitable release sites for the reintroduction of wolves in the area.

Key words: *Canis lupus*, habitat selection, forest cover, landscape analysis, human disturbance, road density, release site.

Résumé : Un certain nombre de caractéristiques doivent être pris en considération dans le choix de sites pour la réintroduction potentielle de loup. Cela inclut le type d'habitat, l'abondance des proies, la perturbation humaine. Plus les conditions seront optimales au site de réintroduction, plus la probabilité de réussite dans l'établissement d'une population de loups sera grande. En utilisant les données du recensement annuel de loups de 2003-2005, nous avons analysé les principales variables d'habitat qui influencent la distribution du loup dans la région de Tver en Fédération de Russie. Nous avons cherché des corrélations par la régression linéaire, entre 6 variables et la distribution du loup dans 36 districts de la région de Tver. Nous avons trouvé la plu forte corrélation positive avec la couverture forestière et une corrélation faible mais néanmoins négative avec la densité humaine : les loups sont présents dans les districts les plus forestiers et les moins peuplés. Nous nous sommes concentrés sur deux districts bien étudiés, Nelidovsky et Toropetsky, et cherché les variables liées à la perturbation humaine qui montraient le plus de différences entre les zones de loups et celles sans loup. Les territoires de loups étaient caractérisés par une densité significativement plus élevée de couverture forestière, et une densité significativement plus basse de villages, que les territoires sans loup: Les barrières naturelles et artificielles telles que rivière, routes et chemin de fer ne semblent pas influencer la présence du loup. Nous concluons en prédisant la localisation de sites de relâcher appropriés dans la région.
Mots-clés : *Canis lupus*, selection de l'habitat, couverture forestière, analyse du paysage, perturbation humain, densité routière, site de relâcher.

Абстракт: При выборе мест возможной реинтродукции волка необходимо учитывать ряд важных характеристик, в частности, условия обитания, наличие достаточной добычи, возможное вмешательство человека. Чем оптимальнее условия на месте реинтродукции, тем выше вероятность успешного создания популяции волков. Используя данные переписи поголовья волков из ежегодного обзора «Зимний Маршрутный Учет» за 2003-2005 годы, мы проанализировали основные переменные параметры среды обитания, которые влияют на распределение волков *Canis Lupus* в Тверской области Российской Федерации. Мы искали, при помощи линейной регрессии, корреляцию между 6-ю переменными параметрами и распределением волков в 36-ти районах Тверской области. Мы обнаружили самую высокую

положительную корреляцию с лесом и низкую но отрицательную корреляцию с плотностью человеческого населения: волки были распространены в более лесных и менее населенных районах. Затем мы сосредоточили свое внимание на 2-х хорошо изученных районах, Нелидовском и Торопецком, и искали переменные параметры вмешательства человека, которые могли бы максимизировать различия между территориями, где присутствуют волки, и теми, где они отсутствуют. Участки, где присутствовали волки, характеризовались значительно более низкой плотностью деревень и более высоким лесом, чем те, где волки отсутствовали. Естественные и искусственные барьеры, такие как река, дороги и железные дороги, кажется, не имеют никакого влияния на пригодность среды обитания. В заключении мы прогнозируем подходящие места для выпуска волков с целью их реинтродукции в этом районе.
Ключевые слова: *Canis lupus*, выбор среды обитания, лес, пейзажный анализ, вмешательство человека, дорожная плотность, место выпуска.

6.2. Introduction

Human development and their dependence on natural resources lead to habitat and animal populations’ fragmentation. Fragmentation is the result of direct habitat destruction and infrastructure development such as roads, railways, and trails. By preventing the movement of terrestrial animals, they reduce the connectivity between populations and the dispersion of young individuals. Populations getting smaller and more isolated are face to greater risk of local extinction due to decrease of genetic variability (Soulé 1987). Roads have also allowed human getting closer to wildlife habitat, which can disturb animals (Lamerenx *et al*. 1992, Mace *et al*. 1996, Primm 1996, Linnell *et al.* 2000), forcing them to adapt their behaviour and thus to spend more energy to avoid people. Roads can also have direct effect on mortality by vehicle collision, and indirect effect by illegal killing thanks to greater access for poachers (Mattson *et al*. 1987, Mech *et al*. 1988, Noss *et al*. 1996).

Around the world, large carnivores have experienced severe decline in past centuries and occur in very small populations when they were not completely exterminated (Breitenmoser 1998). Since management policy (Linnell *et al*. 2001) has improved especially in Europe and North America, large carnivores are about to recover their former ranges naturally, or artificially through reintroductions and translocations (Breitenmoser *et al*. 2001).

Distribution of large carnivores is influenced by environmental and human factors, such food supply, vegetation and human disturbance (Yalden, 1993). Understanding why similar regions show different distribution patterns is necessary when planning recovery or selecting sites for release. A number of important site attributes must be considered when selecting sites for potential reintroduction, including habitat type, prey abundance, competitor and predator abundance, available escape cover, land ownership, linkage to other areas of habitat, and potential human disturbance (Bremner-Harrison & Cypher 2007). The selection of release site plays an important role in release success: the more optimal the conditions are at a reintroduction site, the higher the probability of successfully establishing a population.

Studies based on Geographic Information System (GIS) were used to aid wolf recovery planning in United States (Mladenoff *et al*. 1995, 1999), to predict the wolf recolonization in Italy (Corsi *et al.* 1999), Switzerland (Glenz *et al*. 2001), or Spain (Cayuela 2004), and to understand the factors limiting wolf distribution in Poland (Jedrzejewski et al. 2004, 2005). GIS method was also used to study habitat preferences and distribution of other large carnivores for conservation purposes, such as black bears (*Ursus americanus*) (Mitchell *et al*. 2002) and cougars (*Puma concolor*) (Riley & Malecki 2001). In this paper, we present the results of habitat analysis variables associated with wolf distribution in the region of Tver in west Russia using partly GIS.

The wolf population in Tver region is one of the densest in Russia although the numbers are lower than in past years. Territory size ranges from 150 to 400 km² and there is often free territory between two packs. The dispersion rate of the young is high: no one-year-old young stay with the parents. Thus a pack is often constituted by a breeding pair and the offspring of the year, with an average of 6.8 wolves per pack. Moose and wild boar are the main prey animals; beaver, hare, dog raccoon and other small mammals are killed on occasion. Despite its low population density, humans are present through their activities: meat factories, husbandry, traffic, hunting… Thus, wolves in the area are synanthropic: they may find meat remains near the slaughterhouse and they often come to villages where they may kill livestock or dog. In such a country where wolf hunting is permitted all year round by all means, we may assume that wolf mortality is mainly caused by humans. Harvest by hunters and collision with train or car are the primary causes of wolf death.

Studies in the Great Lakes region in North America showed that wolves most often occurred in forests and strongly avoided agricultural land (Conway 1996) and wolf territories were characterized by low density of roads (0.23 km/km^2) and humans (1.5 inhabitants/km^2) (Mladenoff *et al*. 1995). In Poland, Jedrzejewski *et al*. (2004) showed that wolves avoid areas with dense network of motorways and railways. And wolf territories were characterized by high forest cover (64%) and low number of villages and towns (Jedrzejewski *et al*. 2005). Since the main results of previous studies show the human impact on wolf with the emphasis on predator-human relationships, we expect the variables reflecting human disturbance to be the more relevant for habitat suitability of wolves.

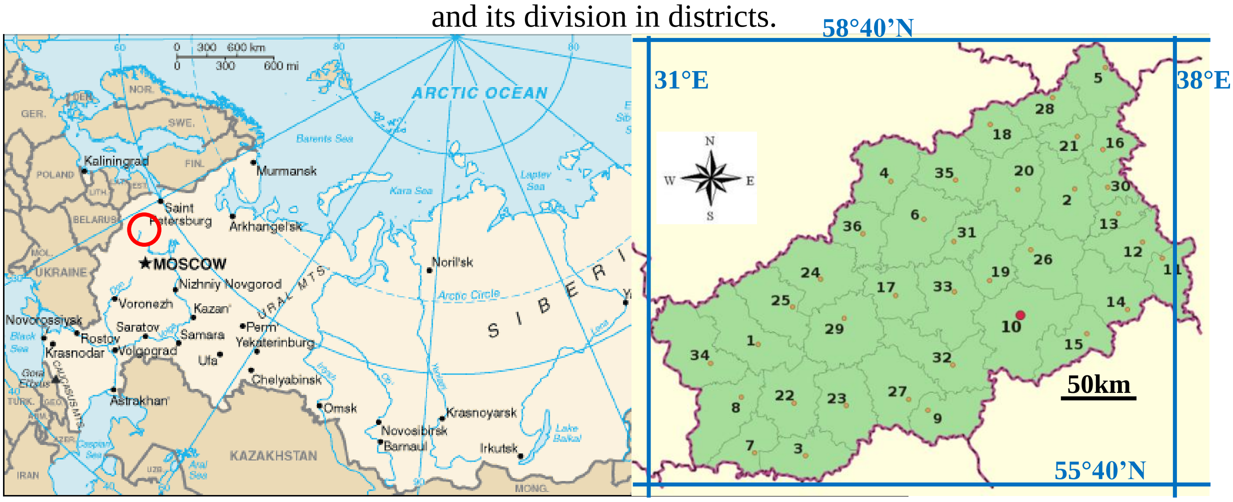
Habitat suitability analyses for conservation programmes are usually made on an area where the species is known to be present. The model can then be extrapolated to a larger area, to predict recovery, dispersion, and needs for habitat and species protection. The aims of our study were (1) to determine the main habitat factors that influence the distribution and numbers of wolves, so as (2) to predict potential sites for wolf release.

6.3. Material and methods

6.3.1. Study area

The Tverskaya Region is situated in the north-western part of European Russia between Moscow and St. Petersburg and it covers an area of 84,000 km^2. Its geographical location is between 55°40’-58°40’ north and 31°00’-38°00’ east (Fig 6.1). The climate is continental with temperature ranging from average –10°C in January to average +17°C in July. Annual precipitation varies between 550 and 750 mm. There is a constant snow cover from the end of November until the end of April, with an average height of snow of 50 cm.

Fig 6.1: Geographical situation of Tverskaya Region in Russian Federation and its division in districts.



# district	Russian name	Latin transcription	# district	Russian name	Latin transcription
1	Андреапольский	Andreapolsky	19	Лихославльский	Likhoslavlsky
2	Бежецкий	Bezhetsky	20	Максатихинский	Maksatikhinsky
3	Бельский	Belsky	21	Молоковский	Molokovsky
4	Бологовский	Bologovsky	22	Нелидовский	Nelidovsky
5	Весьегонский	Vesiegonsky	23	Оленинский	Oleninsky
6	Вышневолоцкий	Vishnevolotsky	24	Осташковский	Ostashkovsky
7	Жарковский	Zharkovsky	25	Пеновский	Penovsky
8	Западнодвинский	Zapadnodvinsky	26	Рамешковский	Rameshkovsky
9	Зубцовский	Zubtsovsky	27	Ржевский	Rzhevsky
10	Калининский	Kalininsky	28	Сандовский	Sandovsky
11	Калязинский	Kaliazinsky	29	Селижаровский	Selizharovsky
12	Кашинский	Kashinsky	30	Сонковский	Sonkovsky
13	Кесовогорский	Kesovogorsky	31	Спировский	Spirovsky
14	Кимрский	Kimrsky	32	Старицкий	Staritsky
15	Конаковский	Konakovsky	33	Торжокский	Torzhoksky
16	Краснохолмский	Krasnokholmsky	34	Торопецкий	Toropetsky
17	Кувшиновский	Kuvshinovsky	35	Удомельский	Udomelsky
18	Лесной	Lesnoy	36	Фировский	Firovsky

The province is home to 1.65 million people of which 1.2 million live in the cities, alone the capital Tver numbering ~470 000 inhabitants. Population density averages 20 people/km^2, but since 73% of the inhabitants live in cities, the density in the rural areas never exceeds 5 people/ km^2.

The region is divided into 36 districts and each district is subdivided into 10 to 20 administrations. Besides the capital Tver, the big cities are the capitals of each district, with about 5 000-15 000 inhabitants. Remaining human settlements are considered villages, with in general less than 1000 inhabitants.

41,933 km^2 (~50%) of the province are covered by southern boreal forest, with spruce *(Picea abies)*, pine *(Pinus sylvestris)*, birch *(Betula pendula)*, aspen *(Populus tremula)*, and alder *(Alnus incana)* as the dominant species. The rest of the area consists of swamps, lakes, and agricultural and urban areas. During recent years, many villages have been abandoned and much cultivated land is growing back to forest. Over fifty years of centralization under the Soviet Union, the village-to-urban population split shifted from 70:30 to 30:70.

The district centres are connected by asphalted roads to the regional centre, Tver, which is on the federal highway Moscow-Saint-Petersburg. The roads network totalizes 15350 km, from which 6562 km are asphalted, and includes 2 federal highways and 1936 inter-municipal highways. Railway operational length makes 1803 km and density of the railway system is 21.4 km/1000km^2 (Fig 6.2).

The region is basically flat, ranging from 61 m to 347 m above sea level. From west to east are found Ploskoshsky lowland, the Valdai hills, the Tver moraine ridge and the Mologo-

Sheksninsky lowland. On the territory flow 800 rivers, totalizing about 17 000 km. The main river is Volga (685 km), and other significant rivers are Zapadnaya Dvina (262 km), Tvertsa (188 km), Medveditsa (269 km), Mologa (280 km) and Mezha (259 km). No less than 1769 lakes (1.4 % of territory) are found in Tverskaya region, including Seliger (260 km^2).

The fauna is typical for the southern taiga. Wolf (*Canis lupus*), brown bear (*Ursus arctos*) and lynx (*Lynx lynx*) are the big carnivores, moose (*Alces alces*) and wild boar (*Sus scrofa*) the most numerous ungulates. Wolves live in 32 of the region's 36 districts: there are no wolves in four districts on the border to Moscow Region. The density of wolves in the western part of the region is higher than in the east, and in general, the density in Tver region is among the highest in whole Russia.

Fig 6.2: Map of Tver region: habitat types, rivers, road and railway networks, main cities.

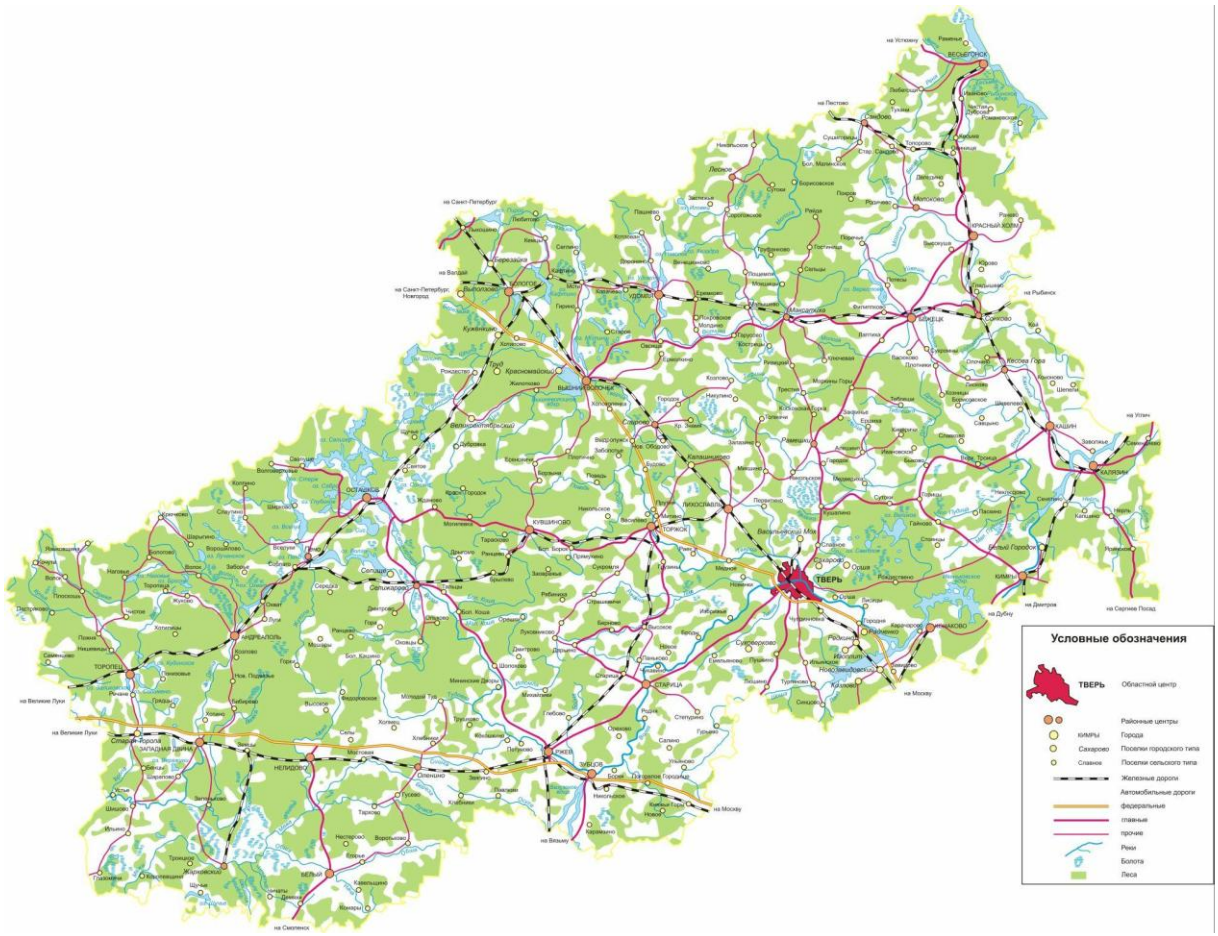
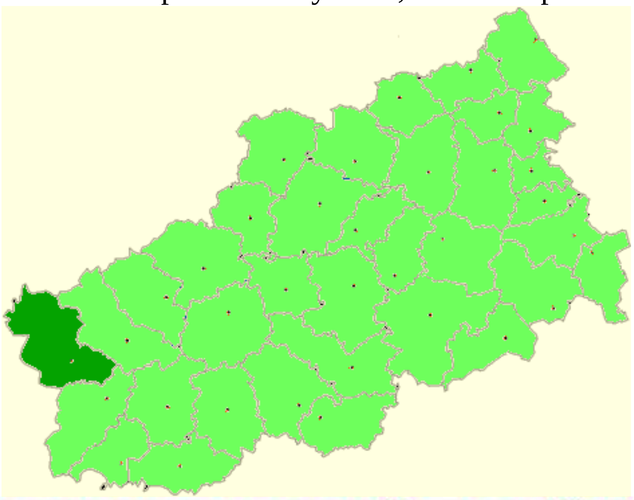


Fig 6.3: Localisation of Nelidovsky district (in dark green) in Tver region and detailed map of the district. Wolf plots are in yellow, wolf-free plots in red.

Fig 6.4: Localisation of Toropetsky district (in dark green) in Tver region and detailed map of the district. Wolf plots are in yellow, wolf-free plots in red.



The districts of Nelidovo (Fig 6.3) and Toropets (Fig 6.4) are situated in the western part of Tver region. Nelidovsky district covers 2632 km^2, where 461 km^2 are protected within the reserve Tsentralno-Lesnoy Zapovednik. The district is divided in 6 settlements, one urbanised area and 5 rural areas. In total live 37500 inhabitants in the district, of which 22886 live in the district capital, Nelidovo. Toropetsky district covers 3373 km^2, where 35 km^2 are protected within the Biological Station “Chisty Les”. The district is divided in 12 settlements, one urbanised area and 11 rural areas. In total live 21460 inhabitants in the district, of which 13033 live in the district capital, Toropets. Details of the surface covered by various land types are given in Table 6.1.

Table 6.1: Land types, their surface and proportion of total surface of Nelidovsky and Toropetsky districts.

	Surface covered in km^2 (% total)			
	Nelidovsky district		Toropetsky district	
Human settlement	458 km^2	17%	165 km^2	5%
Forest	1760 km^2	67%	2352 km^2	70%
Field	306 km^2	12%	750 km^2	22%
Swamp	108 km^2	4%	106 km^2	3%
Total	2632 km^2	100%	3373 km^2	100%

6.3.2. Method analysis

We first proceeded to an evaluation of wolf habitat at the regional scale (Tver region). We looked at the variables associated with wolf distribution and abundance in the 36 districts. We used a set of environmental variables that potentially influence wolf distribution, regarding vegetation cover, prey abundance and human disturbance. We looked for a correlation between these variables and wolf abundance, using linear regression.

Secondly, we focused on the local scale and analysed the variables associated with wolf territories in two well-studied districts, Nelidovsky and Toropetsky. We used two groups, one of known wolf territories and the other of areas where the wolf is absent and we looked for the variables that maximize the differences between the two groups. Wolf sample plots were determined by our knowledge of presence of wolf breeding packs and their territory (tracking and howling surveys). We totalized 12 plots, each of 12x12 km. Twelve wolf-free plots were randomly selected in areas of reported absence of wolves. The plots did not overlap and their size was based on empirical data of wolf territories previous years (Bologov, unpublished data). In total, the plots covered more than 3450 km^2 (about 58% of Nelidovsky and

Toropetsky districts together). For all sample plots, we analysed the following parameters: (1) percent forest cover, (2) river length (we included only large and medium-size rivers), (3) length of motorways, (4) length of secondary roads, (5) length of railways, (6) number of villages (usually <1000 inhabitants). Variables were selected to take into account information relevant to wolf requirements in highly humanised territories, but also according to their availability and degree of coverage for the entire study area (Cayuela 1994). Comparison between wolf plots and wolf-free plots was done with Mann-Whitney U-test.

It is then possible to build a "signature" that best describes the areas where the wolf lives, based on the available environmental variables, and to identify other areas where the conditions are similar to those of the known wolf territories, as potential release sites.

The methodology of comparison wolf areas vs. non-wolf areas has been used in previous studies to evaluate wolf habitat and predict its future settlement (Corsi *et al*. 1999, Glenz *et al*. 2001, Cayuela 2004, Jedrzejewski *et al*. 2004, Jedrzejewski *et al*. 2005). It is assumed that (1) wolves have maintained stable populations in certain territories and not others due to optimal conditions, especially with regard to human influence; and (2) the diversity of environmental and socio-economic conditions within these territories represents the best average conditions for steady presence of the wolf (Cayuela 2004).

6.3.3. Data set

-Regional analysis

The data of wolf distribution in Tver region were obtained at the Federal Hunting Game Survey Service of the Hunting Department of the Ministry of Agriculture. It consisted in results from the yearly winter wildlife track survey called Winter Route Census (WRC) and in questionnaires to the hunting services of each district.

The winter survey takes place in February-March. During two days, the whole staff of hunting services (about 50 persons) walks on determined routes in the territory and marks the tracks found. They cover about 10-20km per day and per person. The first day, they mark every print, old or fresh, and count fresh prints. The second day, they count new fresh prints. Prints collected are then analysed by the Hunting Office and results are set up in tables (Table 6.2).

The Hunting Office also provided us with data about hunted wolves. For each wolf killed, it consists in date, place, technique used, age and sex of the animal when information is available. Densities of prey species (moose, wild boar) were obtained at the Hunting Office, from the Winter Route Census. Human density has been determined through the last inhabitant census in 2010. The distribution of forest, field and swamp comes from official data of each district.

-Local analysis

Environmental variables were measured or counted on the numerical maps. The selected set of variables included 2 regarding vegetation and topography and 4 regarding anthropogenic pressure. It is assumed that taken together these 6 variables provide a good description of the diversity of conditions where wolf is present. A larger set of variables would likely lead to redundancy (Cayuela 1994). Our study did want to use key variables that presumably determine wolf habitat, but uncertainty associated with the lack of potentially informative variables is inevitable (Conroy *et al*. 1995).

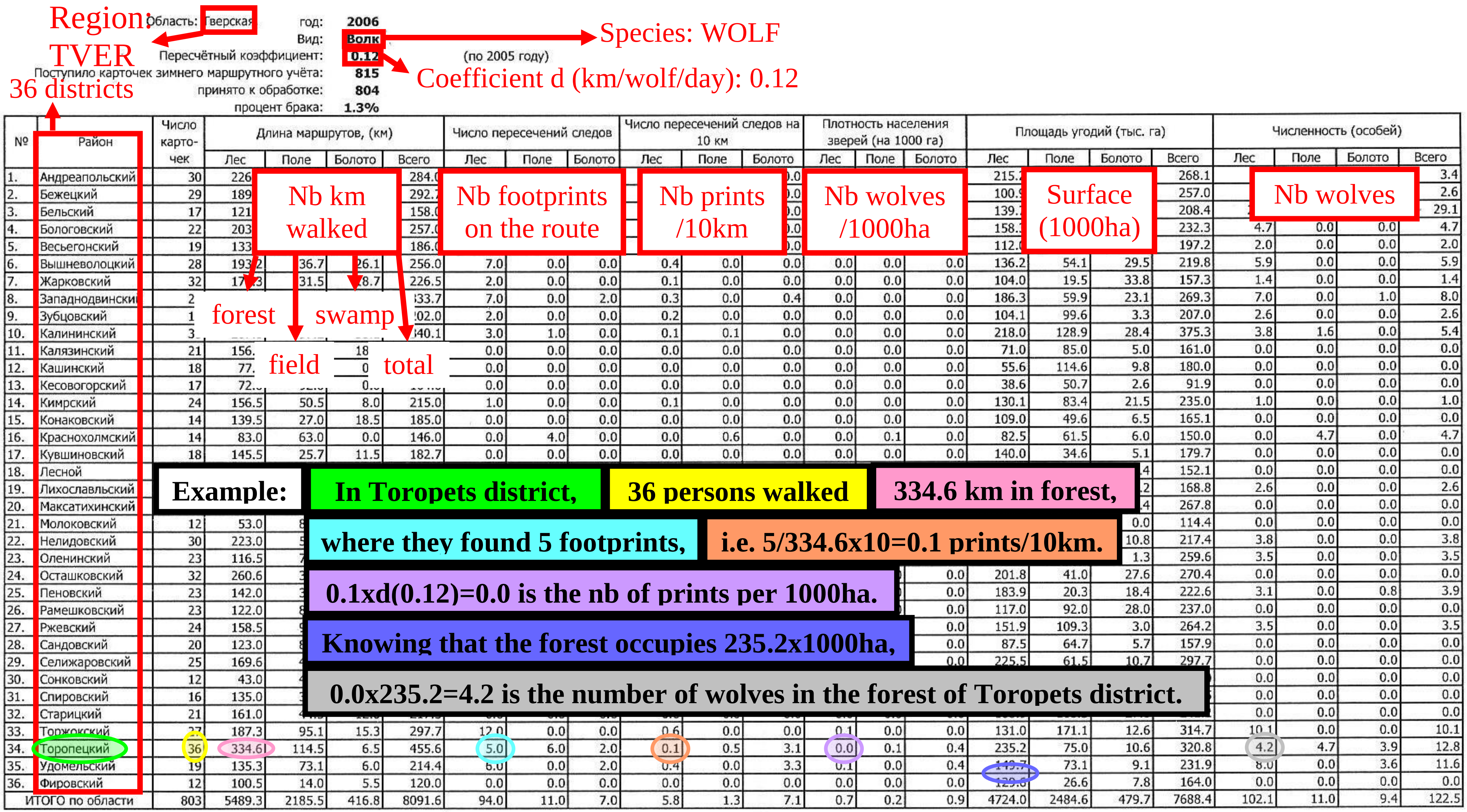


Table 6.2: Example of table got from the Hunting Office: wolf number estimated from winter survey in 2006.

6.4. Results

6.4.1. Wolf abundance in Tver Region

We performed linear regression between wolf density and the 6 variables: forest density, field density, swamp density, wild boar density, moose density and human density, using the data of the 36 districts of Tver region. The wolf density ranges 0.000 to 0.018 animals/km^2, with average 0.003 ± 0.004. The model explained 37.6% of wolf distribution and could be written as following:

Wolf density = 4.679 E-03 + 3.451 E-04 * forest density - 9.972 E-03 * field density - 1.525 E-02 * wild boar density + 2.296 E-02 * moose density - 7.299 E-05 * human density.

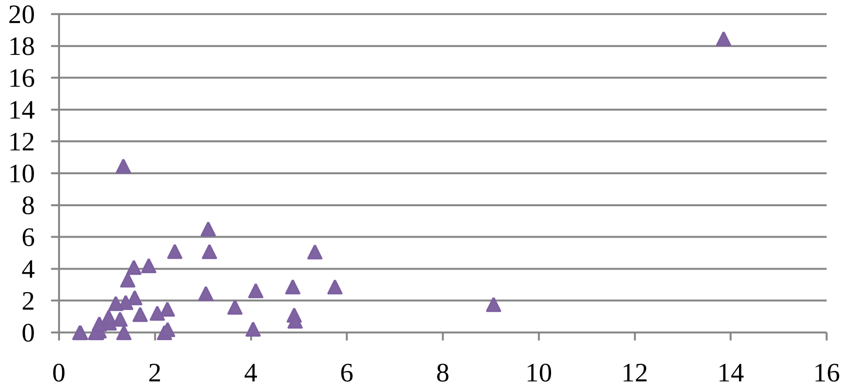
The correlation of wolf density with each variable is given in Table 6.3. The highest correlation happens to be field density, negatively correlated to wolf density with coefficient of -0.42. Wolf density is also negatively correlated to wild boar and human densities with lower coefficients, -0.28 and -0.18 respectively. Wolf density is positively correlated to forest density with a coefficient of 0.40 and in a lower way with swamp density (coefficient of 0.17). The correlation with moose density is close to zero (coefficient of 0.01) (Table 6.3).

Table 6.3: Minimum, maximum, average, standard deviation and correlation coefficient of habitat variables with wolf density in Tver region.

	Forest density	**Field density**	**Swamp density**	**Wild boar density**	**Moose density**	**Human density**
Minimum	0.295	0.062	0.000	0.017	0.028	3.021
Maximum	0.856	0.683	0.215	0.510	0.403	40.775
Average	0.612	0.330	0.058	0.131	0.156	8.901
Deviation	0.146	0.158	0.045	0.100	0.082	6.693
Correlation with wolf density	**0.397**	**-0.415**	**0.174**	**-0.277**	**0.078**	**-0.178**

With the results given relatively high correlation, positive and negative, for forest and field cover respectively, we looked at the relationship between wolf density and the ration forest/field in Tver region (Fig 6.5).

Fig 6.5: Wolf density (individuals/1000km^2) related to the ratio forest/field in the 36 districts of Tver region.



6.4.2. Wolf distribution in Nelidovsky and Toropetsky districts

We compared 12 wolf plots to 12 wolf-free plots regarding 6 variables: forest cover, river length, railway length, motorways and second roads lengths and number of villages. The samples were compared using Mann-Whitney test (Table 6.4). The plots located on Fig 6.3 and Fig 6.4.

Table 6.4: Habitat characteristics of sample plots with wolves (n=12) and those with no wolves (n=12) in Nelidovsky and Toropetsky districts, Tver region, Russian Federation. Mean, standard deviation, minimum and maximum are given. Comparison was done with Mann-Whitney test. **: P<0.05

	Wolf plots		**Wolf-free plots**		**Mann-Whitney test**	
Variables	Mean ± SD	(Min.-Max.)	Mean ± SD	(Min.-Max.)	U	p-value
Forest cover (%)	86.0 ± 6.8	(68-94)	71.8 ± 11.3	(56-97)	124	0.003**
River length (km)	4.1 ± 7.4	(0-18)	11.8 ± 15.0	(0-36)	52.5	0.191
Railway length (km)	0.0 ± 0.0	(0-0)	2.7 ± 4.9	(0-12)	54	0.079
Motorways length (km)	0.9 ± 3.2	(0-11)	1.0 ± 3.5	(0-12)	71.5	1.000
Second roads length (km)	35.3 ± 13.2	(18-57)	42.7 ± 15.8	(4-62)	50	0.214
Number of villages	9.2 ± 2.8	(3-14)	14.4 ± 3.4	(6-18)	15.5	0.001**

We found significant difference of percentage of forest cover between wolf plots and wolf-free plots (P<0.05) with wolves living in areas with 86% of surface covered by forest, whereas 72% in other areas. Significantly fewer villages were found in wolf plots than in wolf-free plots (average 9 vs. 14 villages respectively, P<0.005). We did not found significant differences between the samples for the other variables. But wolf plots had rather less river length than wolf-free plots (4 vs. 12 km respectively). There was no railway at all in wolf territories and average 3 km in other territories. Length of first and second roads in both samples were similar, with 0.9 and 1 km of motorway for wolf-plots and wolf-free plots respectively, and 35 and 43 km of second roads for wolf-plots and wolf-free plots respectively (Table 6.4).

6.4.3. Variables associated with wolf abundance and distribution

Although the samples were quite smalls, the results of this first insight of wolf habitat evaluation show that the variables associated with wolf presence can be classified as following:

-land cover (forest/field): show the strongest correlation with wolf abundance and significant difference with wolf distribution: wolves are more present in forest areas.

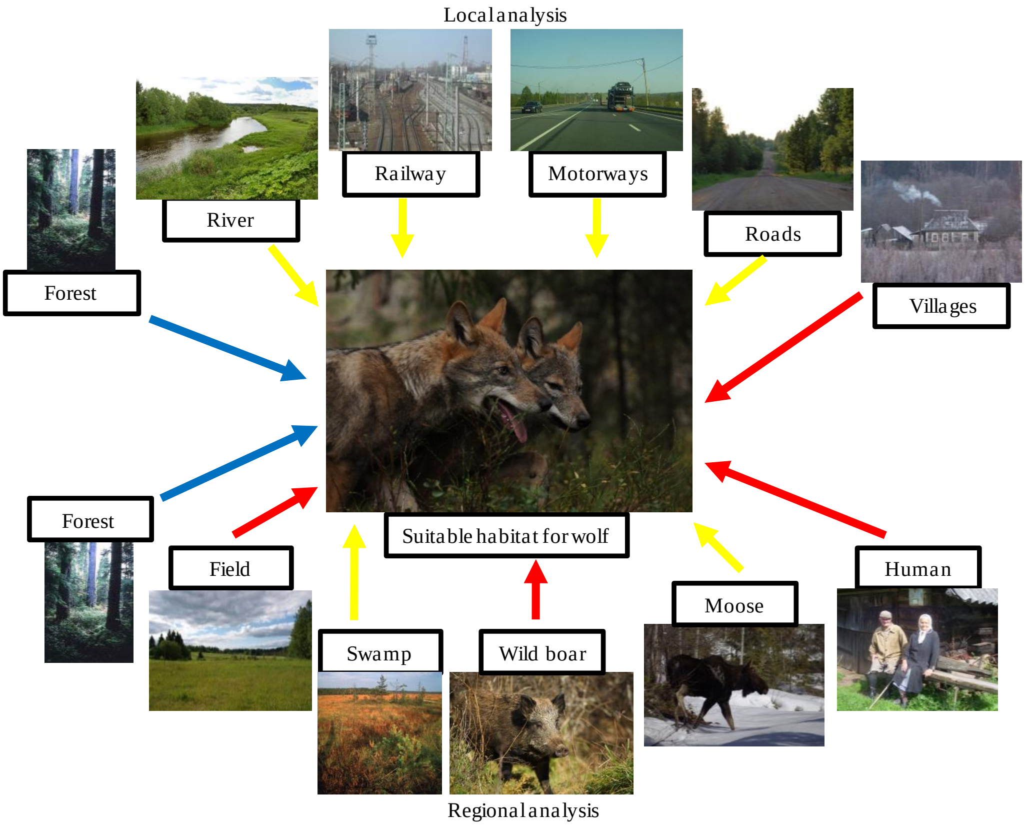
-natural barrier (river): did not show significant difference but was lower in wolf areas.

-artificial barriers (roads, railway): did not show difference and were similar in both areas.

-human settlements (habitants, villages): show relatively low however negative correlation with wolf abundance and significant difference with wolf distribution: wolves are more present in less inhabited areas.

-prey abundance (wild boar, moose): show no correlation (even negative with wild boar) with wolf abundance (Fig 6.6).

Fig 6.6: Habitat variables associated with wolf habitat (**positive**, **negative**, and **neutral** associations) (Photos: L. Becker, V. Bologov, A. Szelest, D. Violett and WWW).



6.5. Discussion

6.5.1. Wolf habitat evaluation

In this study, we found that forest cover was the most important habitat variable influencing wolf abundance in west Russia. Studies in eastern-European countries reported similar results (Jedrzejewski *et al*. 2004, 2005). Type of forest does not seem to influence wolf distribution as demonstrated by Jedrzejewska & Jedrzejewski (1998). A large-scaled study in Europe shows that wolves were more frequently present in areas with 50-80% of forest cover (Mikusinski & Angelstam 2003). In USA, wolf packs occurred in areas with more that 90% of forest cover (Mladenoff *et al*. 1995). Forests provide food resources and shelter, which make them suitable for safe den sites. Wolves are also present is less woody areas, especially in southern Europe, where they were reported in agricultural-forest environment (Boitani 1982, Salvador & Abad 1987). There the risk of depredation on domestic animals is high, because those are more available than wild ungulates (Boitani 1982, Sidorovich *et al*. 2003).

In our study, the prey density was not correlated to wolf distribution. Moose level seems to have no impact at all. This can be explained by the fact that moose are not the favourite prey of wolves in the study area and that they are numerous enough for wolf predation (about 10 moose for 1 wolf) (Bologov, personnal communication). Wild boar density had low, however negative correlation with wolf density. Instead of trying to explain the wolf presence on low-wild boar-dense areas, we may explain the low wild boar density on high-wolf-dense areas by predator-prey relationship. The presence of wolf may control the wild boar population and keep it to a lower level than in other areas where wild boar can multiply. But the control or not of prey population by wolves remain a very discussed subject (Mech & Peterson 2003).

Other natural environmental features such as rivers had little influence on the distribution of wolves in Tver region. In USA, Mladenoff *et al*. (1995) reported a negative relationship between wolves area covered by water. Some authors assume that rivers and lakes can be barriers for the wolves' movements (Haight *et al*. 1998, Harrison & Chapin 1998) but others have proved that wolves can cross even big rivers (Merrill & Mech 2000). In winter, frozen rivers and lakes are often used by wolves to travel easily and quickly (Mech 1994). In this study, the rivers crossing territories were not very large, about 10-20 m, and even wolf pups were often seen crossing them (personal observation).

There is no clear negative relationship between human and carnivore density is not clear (Woodroffe 2000, Linnell *et al*. 2001, Chapron *et al*. 2003). In the United States, wolves preferred areas with < 1.5 inhabitants/km^2 (Conway, 1996). But the growing and spreading human population make wolves occupy suboptimal habitats as well (Mech *et al*. 1988, Mladenoff *et al*. 1999). In Italy, wolves can be seen near human, foraging in garbage dumps (Boitani 1982, Meriggi *et al*. 1996). We found negative, but relatively low correlation between human and wolf densities. Results were more obvious with settlements, as territories of wolves included significantly fewer villages. Except for district centres and very big villages, settlements in Russia are however rather spread and little populated. Wolves are known to cross Russian villages, sometimes without being noticed by inhabitants. Most villages have less than 10 inhabitants and many of them are abandoned or will be in nearest future. The vegetation is growing back quickly on these areas and villages completely disappeared in a couple of years, letting free space to wildlife.

In previous studies, wolves seem to avoid human networks such as motorways, roads and railway. In Poland, the maximum density of roads recorded in wolf samples was 0.38 km/km^2 (Jedrzejewski *et al*. 2004), and in USA, the threshold defining wolf suitable habitat was 0.6 or 0.7 km/km^2 (Mech *et al*. 1988, Fuller *et al*. 1992, Thiel 1995). The fact that the presence of roads can jeopardize wildlife has been well documented for large mammals (Kerley *et al*. 2002, Singleton *et al*. 2002). Roads and railways may be barriers to dispersal and a cause of direct mortality from vehicle collisions. They also cause indirect effects by increasing forest fragmentation and increasing human activities. In Russia however, the density of roads is still low and roads are not modern. Even motorways, except around big cities, are made of 2 ways only. Second roads are very seldom asphalted except when getting closer to cities. Therefore, it is not surprising that we did not find impact of roads on wolf habitat suitability.

6.5.2. Implications for selection of release sites

The aim of this study was to find the variables that best describe wolf habitat, so as to predict releases site for wolf reintroduction. From our results, we would thus select areas with high forest cover and rather low village density. We would look for territories with few roads although the study did not prove this factor to influence habitat suitability. The US Fish and Wildlife Service (1980, 1987) has suggested that the optimum habitat for wolves recovery or reintroduction would have to satisfy the requirements of: (1) a sufficient prey base, (2) suitable denning and rendezvous sites, (3) sufficient space with minimal exposure to humans, (4) maximum 10% of private land ownership, and (5) absence, if possible, of livestock grazing.

It would be important to ensure that the future release site is free of wolf breeding pack. Indeed, wolves are highly sociable animals and conflicts may happen when a stranger individual enters the territory. In 1996, we released 2 wolves on a territory occupied by wolves. They lived for 6 weeks before they were killed by the home pack. The fact that we release young wolves may help in avoiding conflicts since they will display subdominant behaviour towards older wolves they could meet. However, the social factor is better to be checked before release.

Moreover, when selecting areas for reintroduction, it has to be taken into account that wolves are very mobile animals. Areas should therefore consider wolf dispersal corridors and land use zoning (Clarkson 1996, Mech 1996). These factors are quite important, since suitable areas, with nearly the minimum size to assure viable populations, are usually fragmented into smaller units and surrounded by zones with strong human activities and human presence (De la Ville *et al*. 1998). Finally, it will be important to work on public acceptance and sentiments towards wolf in the area of reintroduction.

Establishing areas for reintroduction is a controversial issue in wildlife conservation, in particular when they involve large carnivores. Economic, political, biological, ethical and cultural values all play a role in managing areas and protecting large carnivores (De la Ville *et al*. 1998). That is why well-conducted studies on habitat suitability are needed to increase the success probability of reintroductions. Despite the small sample sizes used in this study and the possible over or under estimation of animal densities by the Winter Route Survey, the present results gave first insight of habitat suitability for wolves in western Russia. The outcome derived from this study may be seen as a method of proposing standards for selection of release site in conservation biology.

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Chapter 7. Conclusion

Chapitre 7. Conclusion

Глава 7. Заключение

7.1. Conclusion générale

L'objectif de cette thèse était d'explorer la réintroduction de loups, avec d'une part leur comportement lors de la captivité et d'autre part leurs aptitudes une fois relâchés ; et en parallèle, d'étudier deux points clés des préparatifs de réintroduction : l'évaluation d'une méthode efficace de suivi et les caractéristiques nécessaires des sites de relâcher. Les études que nous avons menées nous ont permis de démontrer que :

-l'âge de séparation d'avec la meute et la méthode d'élevage influençaient le degré d'audace et d'attachement à l'homme des louveteaux ;

-lors de relâchers avec acclimatation, les individus restaient sur le site et évitaient les mouvements erratiques ;

-le régime alimentaire des jeunes loups relâchés est similaire à celui de leurs homologues sauvages et reflète l'opportunisme et l'adaptabilité des loups ;

-la couverture forestière, la topographie et le comportement du loup influençaient la performance des colliers satellitaires ;

-les variables liées à la présence humaine influençaient le plus le choix du territoire des loups et pouvaient prédire son habitat.

Ces résultats donnent un nouvel aperçu de la réintroduction de carnivores élevés en captivité, et suggèrent la faisabilité d'une telle méthode pour la conservation d'espèces. Je reviendrai ici sur les principales conclusions révélées dans cette thèse.

-La sélection des candidats à la réintroduction sur leurs comportements

Des recommandations antérieures pour la sélection de candidats à la réintroduction soulignaient déjà le besoin de vérifier que les individus présentent les capacités requises à la survie en milieu naturel (Kleiman 1989, International Academy of Animal Welfare Sciences 1992). Un nombre croissant de publications avait également montré l'existence d'une variabilité comportementale individuelle chez les animaux (Clark & Ehlinger 1987, Bolig *et al*. 1992, Mather & Anderson 1993, Hansen 1996, Coleman & Wilson 1998, Mettke-Hofmann *et al*. 2005). Et des études en élevages et zoos avaient suggéré et l'impact des conditions de captivité sur la performance des animaux (Spoolder *et al*. 1996, Dutton *et al*. 1997, Carlstead 1999, Wielebnowski 1999, Wemelsfelder *et al*. 2000). En particulier, on connaissait l'importance de la dimension audace-timidité dans la personnalité des animaux (Wilson *et al*. 1994) et son possible lien avec la survie (Bremner-Harrison et al. 2004). En nous penchant sur la question, nous avons pu confirmer le poids de l'audace parmi les traits comportementaux. Nous avons trouvé un lien entre les comportements audacieux et d'attachement à l'homme. Enfin, nous avons suggéré l'influence de deux critères majeurs, à savoir l'âge de séparation de la meute et la méthode d'élevage, sur ce comportement (chapitre 2). Ces résultats ont des implications sur (1) la sélection des candidats à la réintroduction, et (2) les méthodes d'élevage à utiliser. L'audace semble être le critère prioritaire à évaluer chez les candidats à la réintroduction, soit par notation d'observateurs, soit par test (piégeage par exemple). En ce qui concerne la méthode d'élevage, pour des canidés sociaux comme le loup, il semble important de retarder l'âge de séparation de la meute à au moins 6 semaines. Dans les cas contraires, le placement avec des loups adultes donnera également des individus farouches face à l'homme.

-Le relâcher avec site d'acclimatation

Le relâché d'un animal en territoire inconnu, qu'il s'agisse de translocation d'individus sauvages, de réintroduction d'individus élevés en captivité ou de réhabilitation d'individus orphelins, produit souvent des comportements anormaux et des mouvements erratiques et est associé à une forte mortalité (Bright & Morris 1994, Robertson & Harris 1995). D'après Moore & Smith 1991, le relâcher avec site d'acclimatation, c'est-à-dire avec une période de captivité sur le site de relâcher et l'apport en nourriture et protection sur le site après le relâcher, réduirait les comportements anormaux et la mortalité. En milieu sauvage, les loups quittent la meute parentale vers 11-24 mois et la dispersion a lieu par étapes, avec plusieurs incursions exploratoires en territoire étranger avant de quitter définitivement la meute (Fritts

& Mech 1981, Van Ballenberghe 1983, Peterson *et al.* 1984, Messier 1985, Potvin 1988, Fuller 1989, Gese & Mech 1991). En suivant par télémétrie satellitaire des loups relâchés sans et avec site d'acclimatation, nous avons pu montrer que ces derniers avaient un comportement plus proche de leurs homologues sauvages. Les individus relâchés avec acclimatation ont tendance à rester plus longtemps sur le site, à parcourir de plus courtes distances et à faire de fréquents allers-retours, alors que les individus relâchés sans acclimatation parcourent des distances importantes dès les premières semaines, entrecoupées d'arrêts de quelques jours (chapitre 3). Par ces résultats, nous recommandons fortement l'utilisation de site d'acclimatation dans le relâcher d'individus pour la réintroduction.

-Le régime alimentaire des loups réintroduits

On savait que le comportement prédateur était instinctif chez les canidés, où les jeunes réagissent au mouvement de la proie, stimulus dans l'orientation, l'approche et la poursuite (Fox 1969, Badridze 2003). Mais l'entraînement avec les parents devait également jouer un rôle important dans l'apprentissage de la chasse et la réussite de la mise à mort (Fox 1969). Il était donc intéressant de comprendre comment des louveteaux orphelins élevés en captivité se nourrissaient pour survivre. Contrairement aux préjugés qui voudraient que des carnivores élevés en captivité ne craignent pas l'homme et s'attaquent au bétail, l'étude a montré que les loups réintroduits se nourrissent principalement de proies sauvages : sanglier, élan et lièvre, variable, puis de différents mammifères de taille moyenne et de petits rongeurs, ainsi que oiseaux et reptiles. Les loups ont aussi consommé une grande quantité de matière végétale, et ont occasionnellement tué des animaux domestiques, adaptant leur comportement alimentaire aux saisons (chapitre 4). Nos résultats ont montré que les loups réintroduits avaient un régime alimentaire similaire à celui de jeunes loups sauvages et sont donc capables de survivre en milieu sauvage.

-L'utilisation de collier satellite pour le suivi

La télémétrie a permis de grandes avancées en recherche sur la faune sauvage, avec la possibilité de localiser les animaux à tout moment (Mech & Barber 2002). Les colliers GPS ont équipé les loups du monde entier, en Amérique et en Europe (Bourgeois 2009), mais aucune étude n'avait encore été menée dans cet immense pays forestier qu'est la Russie. Constructeurs et scientifiques ont montré à plusieurs reprises la baisse de performance et de précision des colliers due à la couverture forestière ou à la topographie (Rempel *et al.* 1995, Edenius 1997, Rempel & Rodgers 1997, Dussault *et al.* 1999). Mais les résultats sont difficilement extrapolables et peu d'études se sont placées en condition de terrain, à savoir sur l'animal (Johnson *et al*. 2002). Nos études ont montré que les modèles GPS/GSM collar Lotek WildCell 4400S et GPS/Argos collar ES-PAS Pulsar fonctionnaient très bien en zone ouverte et accusaient une diminution de la performance sous canopée et en zone encaissée similaire aux modèles précédemment étudiés. De plus, la vitesse affecte le temps d'acquisition d'un point et la position de la tête du loup diminue le taux de succès lorsque l'animal dort la tête sur le côté. Le modèle Lotek s'avère peu utilisable en forêt boréale russe où la couverture GSM est pauvre, alors que le modèle ES-PAS n'a pas montré d'échec dans la transmission des données (chapitre 5). Pour optimiser le suivi satellitaire d'animaux relâchés, le chercheur devra s'assurer que le modèle est adapté aux conditions environnementales et logistiques de la zone d'étude, et au comportement, à l'activité et au confort de l'espèce équipée.

-Les variables définissant l'habitat du loup

Avec le retour progressif des grands carnivores dans leur aire de répartition d'origine et le besoin de gérer les populations, les études d'évaluation d'habitat se sont multipliées pour identifier les besoins des espèces en termes d'habitat et prédire les territoires de leur retour ou les zones à protéger (Corsi *et al.* 1999, Glenz *et al*. 2001, Riley & Malecki 2001, Mitchell *et al*. 2002). Un des facteurs négatifs dans la distribution des grands carnivores serait les barrières, naturelles ou artificielles, qui augmentent la fragmentation d'habitat, perturbent la dispersion des animaux et isolent les populations avec le risque final d'extinction locale (Zimmermann 2004). Notre étude s'est intéressée aux caractéristiques définissant au mieux l'habitat du loup en Russie occidentale, afin d'optimiser le choix des sites de relâcher lors des réintroductions. Sur des variables incluant le type d'habitat, l'abondance des proies, la perturbation humaine, nos résultats ont montré que couverture forestière et la densité humaine avaient le plus d'impact, la première positivement, la seconde négativement (chapitre 6). Les barrières telles que rivière, routes et chemin de fer, n'avaient que peu d'impact, mais ceci peut s'expliquer par leur faible développement en campagne russe. Nous recommandons donc le choix de site avec une forte densité forestière et une faible densité de villages, sans oublier l'absence de meute de loups, pour les relâchers futurs.

7.2. Approche multidisciplinaire

Fait peu souvent souligné, la réintroduction nécessite une approche multidisciplinaire. Nous l'avons vu à travers cette thèse, l'étude d'un projet de réintroduction demande de travailler sur le comportement des animaux, leur physiologie et écologie, mais également sur des domaines plus techniques tels que les systèmes de suivi des individus, ou encore la modélisation de leur habitat. Jongler entre ces différentes disciplines de la biologie animale n'est pas toujours chose aisée. Nous verrons plus bas qu'une équipe constituée d'experts dans différents domaines est vivement recommandée. Mais la réintroduction ne nécessite pas uniquement des connaissances en biologie. Le facteur humain y est très présent et des connaissances en sciences sociales sont les bienvenues. En effet, un programme de réintroduction est souvent intégré dans une coopération entre zoos, administration locale, et organisations non-gouvernementales, qui ne s'entendent pas toujours sur les décisions (Mallinson 1991). Des qualités de médiateur seront également mises à l'épreuve avec la population locale, autre pôle humain de la réintroduction. Les risques de controverse et de conflit sont inévitables lorsqu'on s'attaque aux grands prédateurs. Il faut être capable de trouver les arguments pour convaincre, sans négliger l'opinion de la population locale, aux premières loges de la réintroduction d'animaux potentiellement dangereux. Enfin, des aptitudes en sciences de la communication et de l'éducation seront mises à profit lors des couvertures médiatiques et des programmes d'information. Une approche multidisciplinaire est donc nécessaire, pour intégrer les connaissances en biologie et en sociologie dans un même projet de conservation (Clark *et al*. 2001).

De plus, pour mener à bien un programme de réintroduction, un travail à plusieurs niveaux est indispensable, afin de passer des recommandations théoriques à leur mise en pratique sur le terrain. Le travail de recherche des biologistes de la faune sauvage se terminent souvent par une série d'implications ou une liste de recommandations pour améliorer la gestion de telle ou telle ressource. Mais ces suggestions son rarement appliquées sur le terrain (Zimmermann 2004). Une raison à cela est que les suggestions sont rarement accompagnées d'instructions pour leur mise en pratique et pour l'évaluation de leur efficacité (Morrison *et al*. 1998). Une autre raison est peut-être que chercheurs et gestionnaires s'intéressent à des aspects différents, le chercheur étant plus souvent préoccupé de la valeur de P que du résultat atteint sur le terrain (Zimmermann 2004). Les chercheurs peuvent estimer que la mise en pratique de leurs recommandations n'est pas de leur ressort, mais des projets ont tout de même montré leur rôle crucial et leur nécessaire coopération dans de telles actions. Ainsi, le plan de gestion du lynx en Suisse est un bon exemple de réussite suite à la collaboration entre chercheurs, gestionnaires, preneurs de décision et politiciens (Zimmermann 2004). De part ma participation à tous les niveaux dans le programme de réhabilitation de louveteaux orphelins, de la construction des enclos au nourrissage des animaux, de la collecte de fonds aux campagnes de communication, de la gestion des conflits à l'accueil de volontaires, sans oublier ce travail de recherche, je pense pouvoir donner des implications et recommandations dont la mise en pratique sera aisée et bénéficieront à la biologie de la conservation en général et à la conservation du loup en particulier.

7.3. Implications et recommandations

En plus des lignes directrices de l'UICN relatives aux réintroductions (UICN 1998), plusieurs articles antérieurs ont donné des recommandations concernant les procédures et problèmes des programmes de réintroduction (Kleiman 1989, Chivers 1991, Beck *et al*. 1994, Kleiman *et al*. 1994, Bremner-Harrison & Cypher 2007), car malgré la diversité des espèces avec lesquelles ont été tentées des réintroductions, les questions à prendre en considération sont communes. Elles concernent les coûts, l'habitat disponible, la population source disponible, la logistique, l'impact sur la population locale, la sélection des sites de relâcher, l'organisation et les permis, les stratégies de relâcher, les stratégies de suivi, les critères de succès, la génétique, les comportements, et le manque de documentation. En nous basant sur le programme de réintroduction de loups gris effectué à la Station Biologique « Chisty Les » (Toropestky raion, Tverskaya oblast, Fédération de Russie) depuis 1993, nous avons dressé les principales questions à prendre en considération. Nous retraçons ces étapes, appliquées au relâcher de plus de 60 loups, dont 6 équipés de collier GPS-Argos, entre 1993 et 2011 en Russie centrale.

-Coûts

Le coût est en général le premier facteur limitant d'un programme de réintroduction (Stuart 1991, Stanley Price 1991). Il est donc nécessaire de trouver un apport de fonds qui couvriront toutes les dépenses logistiques (salaires, équipement, transport, monitoring, éducation, etc.), et cela sur le long-terme. A la Station Biologique, le nombre de louveteaux reçus au centre chaque année dépend des fonds disponibles et des capacités de détention et de nourrissage. En moyenne, 5,63 loups ont été recueillis par an, un chiffre très inférieur à l'offre (chasseurs, zoos), et l'on estime à 1000€ les dépenses pour l'élevage d'un louveteau sur un an, frais de nourriture, transport, et maintenance compris, mais suivi post-relâcher non inclus. De plus, le personnel de la Station est entièrement bénévole. La plupart des aides et bourses n'étant versées que pour un an, nous avons créé l'association Lupus Laetus pour assurer le soutien financier du programme de réhabilitation de louveteaux sur le long-terme.

-Habitat disponible

La perte d'habitat étant souvent une des causes du déclin de l'espèce que l'on cherche à réintroduire, le manque d'habitat peut également être un facteur limitant. Les territoires appropriés et disponibles peuvent être limités. Pour augmenter les chances de succès, le site de relâché devrait être protégé et contrôlé (Kleiman 1996). Il faudrait également tenir compte de la capacité du territoire à supporter la population nouvellement implantée. Des études préalables de l'écologie de l'espèce et la modélisation peuvent aider à déterminer si un territoire est propice à la réintroduction d'une population et à sa viabilité sur le long-terme. A la Station Biologique, les loups sont relâchés dans une zone protégée de 35km^2 qui leur assure une protection contre les chasseurs les premiers temps.

-Population source disponible

Les animaux relâchés doivent remplir un certain nombre de critères (âge, sexe) pour optimiser leurs chances de survie (Yalden 1993, Sarrazin & Legendre 2000). Les individus devraient provenir préférentiellement du milieu naturel plutôt que de la captivité, sans que prélèvement d'individus d'une population source ne mette celle-ci en péril, en particulier pour les espèces rares (Reading & Clark 1996). A la Station Biologique, les individus proviennent des chasseurs, qui vident les tanières lors de chasse à la tanière, ou de zoos qui ne peuvent garder les portées par manque de place. Nous préférons travailler avec des loups captifs pour ne pas entretenir la chasse à la tanière, même si celle-ci est très ancrée dans la culture cynégétique russe.

-Logistique

La plupart des programmes de réintroduction sont menés par une collaboration de plusieurs organisations, gouvernementales et non-gouvernementales, universitaires et zoologiques. Une organisation à plusieurs niveaux peut être bénéfique, à condition que l'équipe de travail reste gérable. Les organisations devraient clairement définir leur rôle et leur engagement dans le programme, pour éviter les conflits de prise de décision et autres manques d'organisation (Reading & Clark 1996). Une équipe diversifiée a l'avantage d'offrir des expertises dans les divers domaines qui couvrent la réintroduction. Le programme de réintroduction de louveteaux orphelins s'organise en 3 niveaux : la Station Biologique, organisation non commerciale, qui abrite le centre de loups ; l'Institut Severtsov, organisation universitaire, qui fournit des stagiaires et du matériel ; l'Association Lupus Laetus, association à but non lucratif, qui soutient financièrement le programme.

-Impact sur la population locale

Dans des zones de présence humaine, les conflits avec l'homme peuvent menacer le succès de programme de réintroduction, en particulier dans le cas des carnivores. Des attaques sur l'homme ou son bétail, ainsi que la prédation du gibier risquent d'exacerber le conflit entre les carnivores et l'homme (Sillero-Zubiri & Laurenson 2001). Il est donc important d'évaluer l'opinion de la population locale à l'encontre de l'espèce, et l'impact du projet sur la communauté. Dans le meilleur des cas, la population locale devrait être prévenue, éduquée, voire impliquée dans le programme. Dans notre cas, nous avouons ne pas avoir consulté la population au préalable, même si une enquête sociologique a débuté en été 2011 auprès des villageois. De plus, nous travaillons à la création d'un centre d'information et d'éducation sur le loup qui se situera sur place-même. Nous profitons aussi de la renommée de la Station Biologique à travers le programme de réintroduction d'oursons orphelins du Dr. Valentin Pazhetnov.

-Sélection des sites de relâcher

Selon les conseils de l'UICN (1998) pour le choix du site de relâché, il faut s'assurer que (1) les besoins liés à l'habitat et au paysage de l'espèce soient satisfaits ; (2) les causes antérieures du déclin aient été recensées et diminuées ; (3) un programme de réhabilitation de l'habitat soit lancé au cas où l'activité humaine a provoqué une dégradation considérable. Si l'espèce est absente de la zone de relâcher, il faudra en analyser la cause, et éventuellement l'éliminer. Si l'espèce est déjà présente, il ne faudra pas oublier de prendre en compte le facteur social. Deux loups relâchés en 1996 ont été tués par des loups déjà présents sur le territoire. Cela aurait pu être évité en veillant à ce que le site de relâcher n'abrite aucune meute de loups. Eau et nourriture doivent être présentes toute l'année ou les individus relâchés risquent de quitter le site. Il faudra également évaluer la présence de prédateurs ou compétiteurs, ainsi que la présence humaine, son activité et les risques de conflit. Le chapitre 6 de cette présente thèse apportera également des éléments dans le choix des sites de relâcher.

-Organisation et permis

L'UICN (1998) recommande d'évaluer la politique relative à la réintroduction et à l'espèce concernée menée par le pays, et de ne lancer un programme qu'avec l'aval et la participation de toutes les institutions gouvernementales concernées. Cette condition est parfois difficilement remplie, en particulier dans les pays où la protection de la nature n'est pas à l'ordre du jour. Le type de permis nécessaires varie 'une situation à l'autre, en fonction de l'origine des individus, de la législation du pays et de la propriété du site de relâcher. Le cas du programme de réintroduction de louveteaux est un peu différent, car il a été créé justement pour faire face au manque de réglementation censée de la chasse aux loups en Russie. Les biologistes russes demandent le classement du loup en « gibier » depuis les années 1990 (Bibikov 1994).

-Stratégies de relâcher

Les stratégies décidées prennent en compte différents facteurs : entraînement comportemental, technique de relâcher, acclimatation, période du relâcher (UICN 1998). Les techniques de relâcher varient et peuvent être classées entre (1) le *hard release*, où les animaux sont pris puis relâchés directement sur le site, sans acclimatation, entraînement, protection ou aide alimentaire ; et (2) le *soft release*, où les animaux sont placés dans des enclos temporaires sur le site de relâcher, et reçoivent par la suite un apport alimentaire et la protection sous forme d'abris. La plupart des programmes utilisent une combinaison des deux. Dans notre cas, nous préférons le *soft release*, pour les loups relâchés à un an. Ils quittent alors leur site d'élevage petit à petit, comme les loups sauvages s'éloignent su territoire parental. Toutefois, comme nous l'avons vu dans le chapitre 3, notre expérience avec 3 loups relâchés en *hard release* a montré des résultats intéressants quant à la dispersion beaucoup plus rapide de ces loups.

-Stratégies de suivi

Un suivi après le relâché est nécessaire pour tous les individus. Cela peut se faire par méthodes directes (marquage, télémétrie) ou indirectes (relevé de traces) (UICN 1998), pour étudier l'écologie et la démographie du stock relâché, étudier les processus d'adaptation à long-terme, analyser la mortalité, intervenir en cas de besoin. De manière optimale, la méthode de suivi utilisée devrait fournir le maximum d'informations en provoquant le minimum de perturbations. Jusqu'en 2009, le suivi des loups relâchés se faisaient par relevé de traces, en raison du manque de moyens financiers. Mais cette méthode est consommatrice de temps, aléatoire et peu précise. Ainsi, les loups relâchés depuis 2010 sont équipés de collier GPS/Argos. Malgré les défaillances précoces des colliers (voir chapitre 3), nous attendons beaucoup de résultats par cette technique. L'évaluation de la performance des colliers dans le chapitre 5 devrait aider les constructeurs dans cette voie.

-Critères de succès

Beck *et al*. (1994) considèrent un programme de réintroduction réussi si la population sauvage atteint 500 individus. Selon ce critère, seul 11% des programmes recensés dans leur étude sont couronnés de succès. Cependant, tout dépend des critères et des buts que l'on se donne. En général, un programme de réintroduction a pour but d'établir une population viable (Griffith *et al*. 1989) avec un taux de croissance positif (Matson *et al*. 2004). Pour les espèces au taux de reproduction faible, le succès ne pourrait être visible qu'à long-terme. Le programme peut alors se fixer des critères de succès intermédiaire, mesurés à chaque étape de la réintroduction. Ainsi, dans notre cas, nous avons défini les critères de succès comme suit : des individus capables de survivre sans le soutien de l'homme, qui ont peur de l'homme et n'attaquent pas le bétail, qui se reproduisent dans le milieu sauvage. Ce dernier n'a pu encore être vérifié. De plus, la prise de conscience par la communauté de l'importance du loup dans son écosystème, fait également partie de nos critères de réussite.

-Génétique

L'isolation d'une population est souvent le résultat de fragmentation d'habitat qui restreint le flux de gènes et le maintien de variation génétique (Storfer 1999). Une population au nombre d'individus restreints est plus touchée par la consanguinité et plus vulnérable aux maladies. L'hybridation avec d'autres espèces peut également menacer une population. La perte de variation génétique ou l'expression de gènes délétères augmentent le risque d'extinction de l'espèce (Frankham 1995). C'est pourquoi une grande attention doit être portée sur la composition génétique des individus réintroduits. En particulier, dans les cas où seule la population captive est disponible pour la réintroduction, il faudrait s'assurer que cette population présente un pool génétique varié et ne souffre pas de consanguinité. Pour plusieurs espèces (le putois à pieds noirs (*Mustela nigripes*), le loup rouge (*Canis rufus*), le condor de Californie (*Gymnogyps californianus*), oryx d'Arabie (*Oryx leucoryx*), et l'oryx algazelle (*Oryx dammah*)), il a fallu créer un programme de reproduction en captivité à partir des derniers individus sauvages (Seal 1991). Dans tous les cas, que les individus relâchés soient d'origine captive ou sauvage, il faudrait s'assurer qu'ils présentent un maximum de variabilité génétique, pour éviter le risque d'effet fondateurs (Griffith *et al.* 1989, Reading & Clark 1996). Dans notre cas, nous essayons au maximum de relâcher les individus dans leur aire d'origine. Mais le problème génétique est peu important sachant que l'ensemble des loups de la partie européenne de la Russie sont une seule et même espèce.

-Comportements

La perte de variabilité génétique n'est pas le seul risque du maintien à long-terme de populations captives. Plusieurs études ont montré le manque d'aptitudes nécessaires à la survie telles que la recherche alimentaire, la fuite face aux prédateurs et l'évitement de l'homme, chez des populations captives comparées aux populations sauvages (McPhee 2003, Mathews *et al.* 2005). Ces adaptations des individus à la captivité où nourriture et protection sont assurées et où les contacts avec l'homme sont quotidiens, sont nuisibles une fois les animaux relâchés dans la nature. Un exemple parmi d'autres est l'échec du relâcher de tamarin lion doré (*Leontopithecus rosalia*) qui étaient incapables de s'orienter en terrain inconnu (Kleiman *et al.* 1986). Dans ce contexte, certains programmes ont tenté de préparer les animaux avant le relâcher, soit en leur donnant l'opportunité de faire l'expérience du milieu sauvage (Biggins *et al.* 1999), soit en les entraînant à éviter les prédateurs par des stimuli aversifs (Griffin *et al.* 2000). Kleiman (1996) relève 6 types de comportement que les individus doivent présenter pour être relâchés : (1) évitement de prédateurs, (2) acquisition de nourriture, (3) interaction appropriée avec les con-spécifiques, (4) habilité à construire un abri, (5) habilité à se déplacer sur un terrain complexe, (6) habilité à s'orienter et naviguer dans un environnement complexe. Ces dernières années ont vu croître le nombre d'études sur la variation comportementale et leur intérêt en biologie de la conservation. Tout porte à croire que des différences de personnalité conduisent à des stratégies adaptatives différentes, sujettes à la sélection naturelle (Wilson *et al.* 1994). Un trait comportement important pourrait être le degré d'audace/timidité des individus, qui semble avoir des implications dans la survie des individus relâchés (Bremner-Harrison *et al.* 2004). D'après notre expérience avec les loups, le plus important pour obtenir des individus au comportement approprié est l'âge auquel ils retirés de leurs parents et la méthode d'élevage. Pris entre 3 et 5 semaines et élevés avec des loups adoptifs, ou pris après 6 semaines et élevés seuls, les individus présentent une peur de l'homme (voir chapitre 2). Le comportement de prédation est instinctif et les individus apprendront à chasser par essai et erreur (voir chapitre 4). Ainsi, nous considérons que les loups n'ont pas besoin d'entraînement avant le relâché.

-Manque de documentation

La biologie de la réintroduction est face à un manque de revues bibliographiques concernant les programmes existants. Beck *et al*. (1994) n'ont obtenu des informations que sur moins de 50% des projets de réintroduction connus. Pourtant, il serait important de connaître les raisons des succès et échecs des uns et des autres pour éviter de reproduire des erreurs. C'est dans ce contexte que l'UICN a rédigé les lignes directrices relatives aux réintroductions. Mais celles-ci restent très générales alors que chaque espèce a des spécificités. Dans le cas du loup gris, *Canis lupus lupus*, seul le travail de Badridze (2003) est disponible. Son expérience avec une centaine de loups élevés, dont 22 relâchés en Géorgie, relate les moments importants du développement à prendre en considération dans la méthode d'élevage. Mais son rendement resta faible et de nombreux loups ne purent être relâchés. Ce présent travail de thèse constitue donc un complément non négligeable dans la recherche en biologie de la réintroduction.

-Conclusion

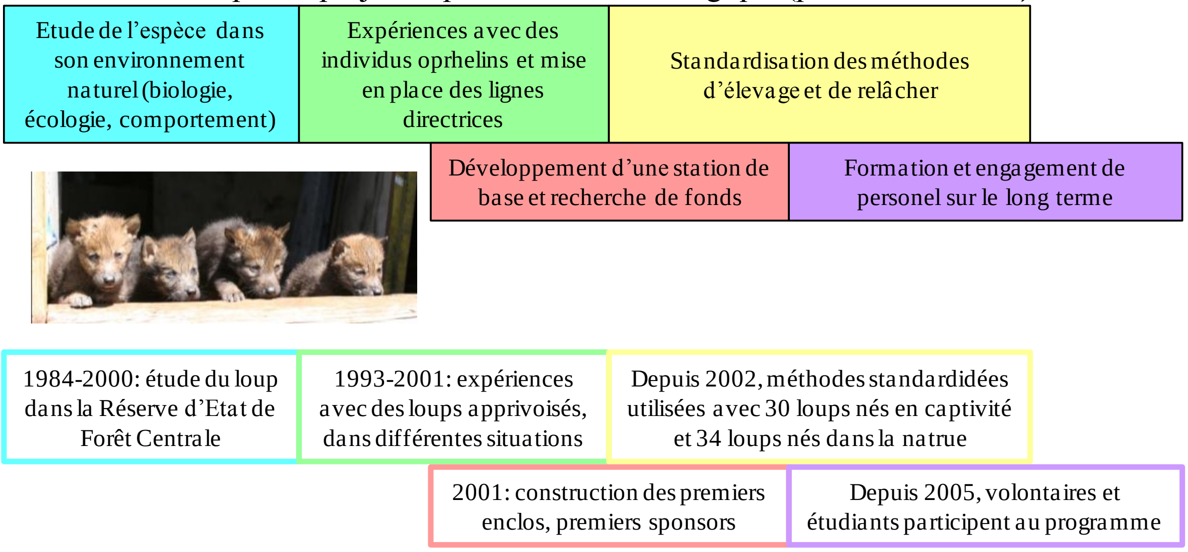
En conclusion, réintroduction et réhabilitation sont des processus complexes, qui demandent un engagement financier sur le long-terme et une collaboration active avec les institutions gouvernementales et non-gouvernementales (Kleiman 1996). D'après notre expérience, les étapes pour faire de ces programmes un succès sont au nombre de 5 (Fig 7.1) :

1. *Avant de commencer* : une connaissance complète de l'espèce est requise. C'est pourquoi il est nécessaire d'étudier les animaux dans leur écosystème naturel. Cela inclut taille et densité de population, dispersion des individus, régime alimentaire et comportement prédateur, mécanismes de défense, comportement sexuel et interactions sociales.
2. *Premières expériences* : il est nécessaire d'étudier en détails le développement. Le meilleur moyen pour cela est de suivre des individus apprivoisés durant leur croissance, et l'on observera le développement des comportements alimentaire, défensif et social. Une attention spéciale doit porter sur les moments des changements dans le développement.
3. *Commencement* : un site et des fonds sont nécessaires. Alors que l'étape 2 est en cours, il faut résoudre les problèmes logistiques. Un soutien financier devra couvrir diverses dépenses (salaries, véhicules, nourriture des animaux, cages et enclos, équipement des animaux pour le suivi post-relâché) sur le long-terme. Il est nécessaire de construire une station de base, pour abriter les animaux, le personnel et l'équipement.

4. *Standardisation* : les études préliminaires sur l'écologie de l'espèce et les études expérimentales sur le développement du comportement servent de bases aux méthodes d'élevage et de relâché. En testant diverses situations à l'étape 2, on peut améliorer la méthode et mettre au point les lignes directrices.

5. *Continuité* : le personnel impliqué doit être formé pour le long-terme. Alors que l'étape 4 est en cours, le programme se développe et nécessite plus de personnel. S'occuper de jeunes carnivores destinés à la réhabilitation requièrent des compétences spécifiques (force physique et émotionnelle, patience, rigueur).

Fig 7.1: Les 5 étapes pour la mise en place d'un programme de réhabilitation, illustré par l'exemple du projet loup de la Station Biologique (photo : G. Müller).



7.4. Perspectives futures

Avec les résultats encourageants de cette thèse concernant la réintroduction de loups élevés en captivité, les perspectives pour la biologie de la conservation sont grandes. Chacun doit pouvoir trouver des recommandations pour son propre programme de réintroduction et l'adapter à l'espèce étudiée. Je présenterai ici brièvement une application réellement directe des résultats de cette thèse. Après avoir été discuté avec les intéressés, le projet comme présenté ci-dessous est au point mort. Je garde l'espoir que la parution de ces résultats pourra le faire avancer.

Le projet concerne le sauvetage de la population scandinave de loups, en situation génétique critique. On croyait la population éteinte dans les années 1970, mais des individus ont été observés en Suède en 1983. La population a cru de 8 à 200 loups de 1990 à 2009. Mais la consanguinité y est élevée et la population est menacée d'extinction (Liberg 2005). La population scandinave de loups s'est en effet développée à partir d'un seul couple reproducteur, avant qu'un mâle migrant apporte de la variabilité génétique en 1991 (Vilà *et al*. 2003). La population se trouvant isolée, située à 800km de la plus proche population finno-russe de loups, ce type d'événement salvateur est rare. Face à cette situation critique, les experts suédois cherchent des solutions pour améliorer la situation génétique de la population. Parmi les options possibles, les corridors écologiques semblent difficiles à créer en raison de la grande distance entre les populations. La translocation d'individus depuis des pays limitrophes se heurterait à la stricte réglementation suédoise sur la mise en quarantaine. L'insémination artificielle de femelles sauvages n'a pas encore été suffisamment étudiée. Côté suédois, l'idée de l'adoption croisée, c'est-à-dire d'échanger des louveteaux de portées différentes, a donc été avancée. Il s'agirait d'un côté d'élever un groupe de louveteaux (mâle et femelle provenant de zoo et mâle et femelle provenant de chasseur), selon les méthodes utilisées à la Station Biologique. Un couple reproducteur pourrait se former au sein de ce groupe et leur portée serait utiliser dans l'adoption croisée avec des louveteaux de meutes sauvages. Ce scénario prendrait beaucoup de temps, sachant que les loups ne sont en général sexuellement matures qu'à deux ans. De plus, l'adoption croisée a été peu étudiée, et l'on ignore l'efficacité de la méthode. Une tentative avec des loups dans le Wisconsin a échoué mais les louveteaux étaient sûrement trop âgés (Schultz *et al*. 2007). Sur des coyotes (*Canis latrans*) captifs, l'expérience a été réussie en remplaçant la totalité de la portée et ce avant 6 semaines (Kitchen & Knowlton 2006). Face à ces possibles difficultés, nous suggérons la méthode de réintroduction employée à la Station Biologique : prendre des loups nés en captivité ou en milieu sauvage après 6 semaines, les élever avec le minimum de contact humain directement sur le futur site de relâcher, et les libérer à l'âge d'un an.

Le projet s'est arrêté au stade de la discussion et la dernière option ne sera probablement pas la première retenue, en raison de nos résultats trop récents, du scepticisme de la communauté scientifique quant à la réintroduction d'animaux captifs, et de la frilosité du public quant au relâcher de carnivores passés entre les mains des hommes. Cela reste cependant excitant d'imaginer la réalisation d'un tel projet pour sauver la population de loups scandinave ou toute autre population de canidés à travers le monde.

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