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Predators detect the welfare of their potential prey and cull those that are poorly

A.S. Severtsov[1], M.L. Rosenzweig[2]* and A.V. Shubkina[3]

[1]*Biological Faculty, Moscow State University, Moscow, Russia,*
[2]*Evolutionary Ecology Ltd, Tucson, Arizona, USA and*
[3]*Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia*

ABSTRACT

Aim: Test the hypothesis that predators influence the fitness of their prey by taking prey individuals disproportionately in poorer condition.

Questions: How do wild, herbivorous animals taken by predators in nature differ from those that survive?

Organisms: Wild prey – *Saiga tatarica* (an antelope) and *Lepus europaeus* (brown hare). The predator – trained hunting dogs (sighthounds).

Methods: We compared the prey taken by sighthounds in the field to those shot by human hunters. We conducted pathological, anatomical, and microbiological studies and compared the results for prey taken by sighthounds with prey taken by human hunters. We used GPS technology to track, second by second, the speed and direction of hounds that were hunting. To determine the concentration of microorganisms on their skin, we studied animals killed by human hunters as well as by hounds. Finally, we studied the reaction of the hounds to olfactory stimuli of bacterial origin.

Results: The hunting success of the hounds is well below 50%. The predator must try repeatedly to capture its prey. Animals taken by hounds do not differ by sex, age, size or any movement parameter compared with those shot by humans. But the individuals taken by hounds, unlike those shot by humans, include only antelope with abnormal internal organs and hare with low kidney fat and a relatively high concentration of skin microorganisms. The reduced prospects of prey individuals are signalled by odour, formed at least partly by microflora. The hounds sense this odour and respond to it positively.

Conclusions: The moderately low hunting success of predators results in the highly efficient elimination of prey specimens in poor condition. If condition correlates with fitness, then the predator culls specimens with reduced fitness, and that can stabilize the fitness of the prey.

Keywords: adipose capsule, antelope, bacterial odour, brown hare, hunting dogs,
predator discrimination, predator efficiency, prey fitness, sighthounds,
subcutaneous scars.

Correspondence: A.V. Shubkina, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow 117071, Russia. e-mail: annashubkina@rambler.ru

* M.L.R. participated only in the process of writing the paper.

INTRODUCTION

Evolutionary biologists often credit predators with selective elimination of individuals in their prey populations. Although that sounds reasonable, it is not trivial to demonstrate in the field. Although some note that predatory interactions are the main mortality factor for both predator and prey (e.g. Severtsov, 1951, p. 107), often the predator is not the main mortality factor. And the interaction between one pair of predator and prey species may vary in different parts of the same geographical area, in variable seasons and years, and among the sexes and discrete age groups (e.g. Bergman *et al.*, 2006; Valeix *et al.*, 2009). Furthermore, many individuals die due to accidents that cannot be attributed to predation (e.g. Slobodkin, 1961; O'Gara and Harris, 1988; Preisser *et al.*, 2005). Also, the impact of re-established and historically co-existing predator species will differ from each other (Owen-Smith, 2016).

Despite these difficulties, in this paper we show the truth of the oft-assumed relationship. The predator does not kill at random. Instead, it culls the populations of its prey, taking preferentially individuals in poorer condition.

For many reasons, undomesticated predators would provide insurmountable obstacles to their use by ecologists (and we will mention a few along the way). So we use domesticated predators – sighthound dogs – as our model organisms. Although they are domesticated and trainable, this unique group of hunting dogs catch their prey without the help of humans – that is, humans do not first shoot the prey and have the dogs merely collect it. Instead, they search for their prey in the field by being sensitive to movement, and they then chase it down as if they were wild. The American Kennel Club's list of recognized sighthound breeds includes Irish wolfhound, saluki, whippet, greyhound, and borzoi. The FCI (Fédération Cynologique Internationale) also recognizes azawak, deerhound, galgo, magyar agar, Polish chart, slugi, as well as breeds from the former Soviet Union: hortay borzoi, steppe borzoi, tazi, and taigan (Sokolov *et al.*, 2001).

Here, we address the survival component of Darwinian fitness. We do this by comparing the characteristics associated with animals that survive with those that predators eliminate. We also consider whether such features designate fitness directly or instead indirectly by determining other properties that influence hunting success.

METHODS

The model form of predator

We use model predators to determine the selective elimination of two wild herbivorous species. Our data cannot be obtained without model predators because wild ones leave only parts of the carcasses for us to examine.

Our model predators are sighthounds. We employed dogs of the two breeds that are the most popular in traditional Russian hunts: the Russian Longhaired sighthound (Russkaya Psovaya Borzaya) and the Russian Shorthaired sighthound (Hortaya Borzaya), although occasionally we used dogs of two other sighthound breeds (Russian Steppe Borzoi and English greyhound), both members of the same subset of the sighthounds, a group often called 'windhounds'. We used dogs that were chosen, raised, and trained by institute (IPEE RAS) specialists as well as the dogs of private owners.

Sighthounds hunt in open area biotopes, generally steppe or semi-desert. Pursuit usually starts after visual detection (but see Fig. 4). Then the sighthound chases its prey at high speed. This style of hunting is similar to that employed by many terrestrial predators (*Canis lupus*, *C. aureus*, *C. latrans*, *Lycaon pictis*, *Acinonyx jubatus*, *Crocuta crocuta*, etc.). The sighthound's style of hunting makes a wide spectrum of prey susceptible, including herbivores (e.g. hares, rabbits, small and intermediate-sized antelopes) and predators (wolf, coyote, jackal, fox).

Because we settled on the sighthound's hunt as our model system, we had some advantages, including the ability to use entire bodies of data, and the ability to repeat – multiple times – the complete hunting process. A notable disadvantage of the sighthound model is that they do not assess their hunting prospects and so do not select a particular prey in advance; instead, they focus on chasing any prey that come into view.

Some differences in hunting behaviour are most probably due to the history of the breeds. Brief hunts would have taken place in comparatively small, cultivated fields in monoculture, whereas prolonged hunts would have occurred in the steppe zone in fields of enormous size with diverse natural obstacles amongst the terrain and many different types of wild and cultivated plants. Hunts for sport would have favoured hounds that can chase prey at high speed without holding back power. These hounds do not adjust their paths to take account of the traffic, both of the dogs and also the humans riding on horseback. On the other hand, hounds participating in prolonged hunts would have been favoured if they were able to adjust their movement at a wide range of speeds, and change direction according to relief, plants, behaviour of prey, conspecifics, and humans. Windhounds such as greyhounds belong to the dogs of the first type and native Russian sighthounds to the second. We used the native breeds much more often.

The model forms of prey, period of work, and ethical considerations

Free-living saiga antelope (*Saiga tatarica*) and brown hare (*Lepus europaeus*) in their natural habitats constituted our model prey. Both are herbivores. We worked at times of high population density and in areas of high population density, i.e. saiga – 1980s; brown hare – 1980s to the present.

We conducted the hunting of saiga in accordance with official licenses issued by the relevant government authority. We did so during a period of high population density (hundreds of thousands). Professional resident hunters collected animals that had been shot from the state hunting inspection service. The hare hunts took place in line with the programme of support for native Russian breeds (field training and trials). The animals shot as controls were collected from the game bags of legal gun hunters.

Ecosystems and seasons

We worked in natural and partially anthropogenic habitats in the forest steppe and steppe zones of the European part of the former USSR and modern Russian Federation (i.e. the Vologograd, Kalmiik, Rostov, Moscow, Tambov, Voronejsh, and Stavropol districts).

We worked from October to early February. During this period, there were very few weakened animals, no newborns, and no females in the late stages of pregnancy. Experiments did not proceed if there was ice cover or if the depth of snow cover was >15 cm.

Microbiological examination of successfully hunted prey

Post-mortem examinations of brown hare are unreliable because the animals' bodies are often damaged by the dog's jaws or by buckshot. So we performed microbiological studies (Ushakova and Shubkina, 1991; Sokolov *et al.*, 1992, 1993, 1994; Shubkina and Ushakova, 1994) and comparisons of kidney fat (adipose capsule) (Pepin, 1987; Holand, 1992; Stott and Harris, 2006; Vicente *et al.*, 2007; Ezenwa *et al.*, 2009; Millán and Casinova, 2009; Davidson *et al.*, 2012; Chitwood *et al.*, 2013; Santos *et al.*, 2013). 'Total bacterial count' is a marker of host condition, so we compared the concentration of microorganisms with two standard methods: (1) visual counts of mature colonies and (2) spectrophotometric analysis of washouts of the incubated print.

A body of evidence indicates that the microbiota of animals and humans is regulated by stress mechanisms and the immune response (McEwen *et al.*, 1997; Zwierzina, 1999; Hentschel *et al.*, 2000; Fischbach and Bromley, 2001; De Kloet, 2000; Silanikove, 2000; Steinert *et al.*, 2000; Alexander and Hudson, 2001; Akmaev and Grinevich, 2001; Sanders and Straub, 2002; Theis and Stahl, 2004; Padgett and Glaser, 2003; Krokan *et al.*, 2004; Lyte, 2004; Choi *et al.*, 2005; Bailey *et al.*, 2006). Sokolov *et al.* (1990a, 1991) showed that the concentration of skin microorganisms is determined by the host's health. Erofeeva (2015, 2016) demonstrated that the concentration of skin-surface microorganisms indicates the health of dogs and can be used as a non-invasive method to compare their welfare, and we relied on that in our work.

To test the hypothesis that stress mechanisms influence the amount of microorganisms in brown hare, we subjected brown hares to mild stress. We transported them, immobilized them, and shipped them in comparatively small boxes, a procedure that is sufficient to induce a generalized adrenal reaction (Beringer *et al.*, 1996; DeNicola and Swihart, 1997; Grandin, 1997; Boonstra and Singleton, 1999; Boonstra *et al.*, 2002; Marquez *et al.*, 2004).

The microorganisms modify the odour of the prey. This might be important because in the laboratory, we observed that the odour of microorganisms is sufficient to cause the windhounds to change the direction and speed of their motion. And we also know that mosquitoes choose an object to attack in part based on the odour of that object's microorganisms (Lacroix *et al.*, 2005; Nelson and Jackson, 2006; Verhulst *et al.*, 2009, 2011a, 2011b). Thus we evaluated the role of odour (of bacterial origin) in the behaviour of sighthounds.

We performed our experiments in both the field (Shubkina, 2006) and the laboratory. In the field we observed the sighthound's reaction to culture dishes with incubated microorganisms from the hare (we used empty plates as the control).

Recently, we began using an additional internal indicator – the presence of subcutaneous scars. Geist (1986) first mentions this indicator in ungulates and it is present in saiga (Fig. 1b) and in brown hare (Fig. 2b).

Study of motion parameters

We designed and manufactured special GPS-trackers (manufacturer NPF 'Geyser', Moscow) to determine the effect of motion parameters on the success of the hounds. The trackers register coordinates every 1 second and record these on a memory card (file extension *.nmea). This allows for second-by-second positioning, calculation of speed and direction of movement.

We checked the system in the field in several regions (Moscow, Rostov, Volgograd regions). At the beginning of each day of fieldwork, we attached trackers to the dogs with special collars (see Fig. 5b). Observers then recorded and organized events using standard Garmin navigators. Each day, we unscrambled our results using standard procedures to avoid errors due to accidental damage of the devices or the communications system. We used records whose error rate (at least four satellites for proper calculation) did not exceed 5% in 10,000–20,000 lines (Shubkina *et al.*, 2008). We processed the data using freeware programs (U-Blox, file converters, Google Earth) and licensed programs (Excel, Statistica).

RESULTS

Saiga

Sighthound dogs killed saiga antelopes whose internal organs had various abnormalities (Sokolov *et al.*, 1991) (Fig. 1c). Compared with the other animals in the herds, the saiga in our sample did not differ by gender, age or size (Fig. 1a) or by main movement parameters.

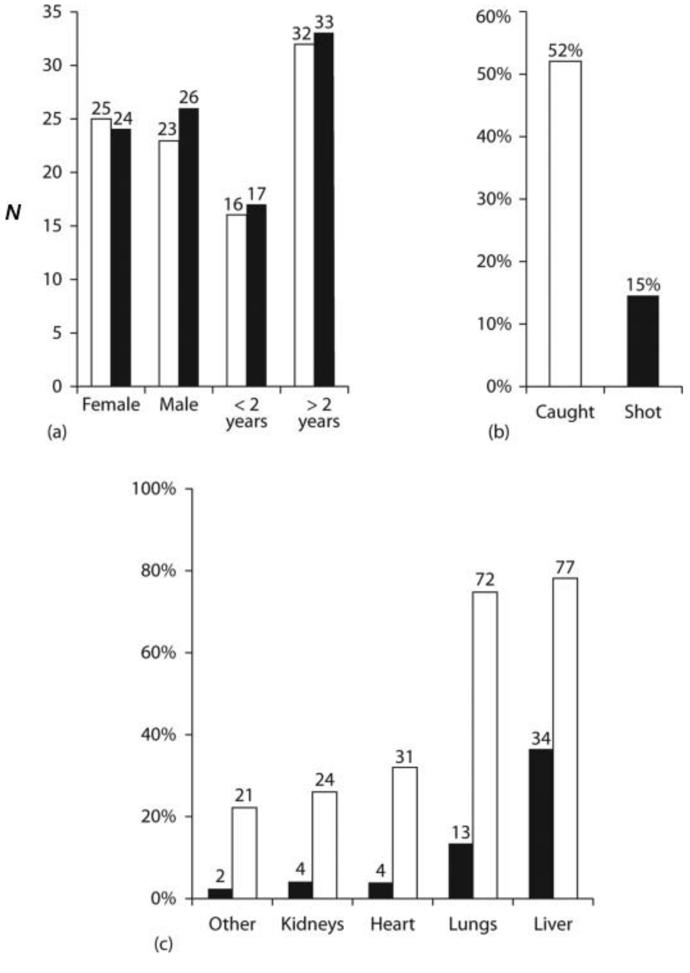

Fig. 1. Saiga antelope: (a) gender and age of shot antelope ($n = 50$) and those caught by dogs ($n = 48$). (b) Subcutaneous scars were less common in shot antelope ($n = 20$) than those caught by dogs ($n = 22$). (c) Percentages of antelope shot and caught whose organs showed abnormalities (shot, $n = 38$; caught, $n = 40$). ■ = shot, □ = caught.

However, humans (both observers and professional hunting inspectors) could discern a probable victim in only 2% of 210 saiga pursuits.

Hunting success is inversely proportional to the number of antelope that appear in the field of view. Sometimes a chase is interrupted – although this is not typical of the sighthound breeds or any individual dogs. Interruptions might occur when hundreds of antelope appear in the field of view, or when the saiga move as a tight group.

Sometimes the sighthounds shift their chase from one antelope to another, especially to a male in the rutting season when the odour of males is quite strong. All this means that a sighthound might modulate its pursuit once started, so that it is much less defined than people believe.

We performed post-mortem examinations on 38 shot and 40 caught antelope. We identified many individuals whose internal organs had various abnormalities. The relative distribution of such abnormalities did not differ between the two groups (Fig. 1c). But antelope caught by dogs were significantly more likely to have abnormal internal organs than those shot by humans (Student's *t*-test, $P < 0.025$) (Fig. 1b). Individuals with abnormalities were prevalent (Student's *t*-test, $P < 0.001$) among caught antelope, whereas they represented only about one-third of shot antelope.

Brown hare

The proportion of hares with low kidney fat caught by dogs (Student's *t*-test, $P < 0.05$; $P < 0.025$) was significantly higher than that of hares that were shot (Fig. 2a). Subcutaneous scars (Fig. 2b) were present in 27% of the caught group ($n = 26$), whereas none were observed in shot hares ($n = 15$) (Blohina, 2016). The concentration of skin microorganisms (Fig. 3a) was also significantly higher in hares caught by dogs (Student's *t*-test, $P < 0.01$) (Fig. 3b). But microbial indicators of 'stressed' hares did not differ from those of 'caught' hares.

In the laboratory (dogs, $n = 43$; tests, $n = 611$), the odour of microflora (culture dishes with incubated microorganisms instead of controls) was found to influence the prevalence

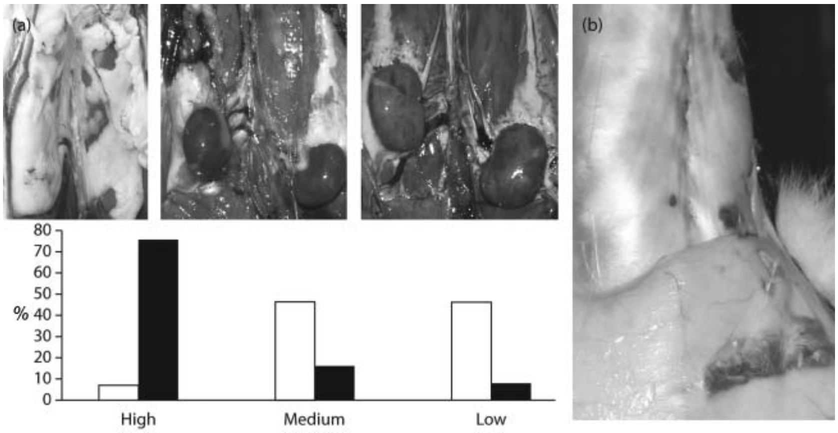

Fig. 2. Brown hare: (a) kidney fat of caught hare ($n = 56$) and shot hare ($n = 37$). ■ = shot, □ = caught. (b) Old subcutaneous scars.

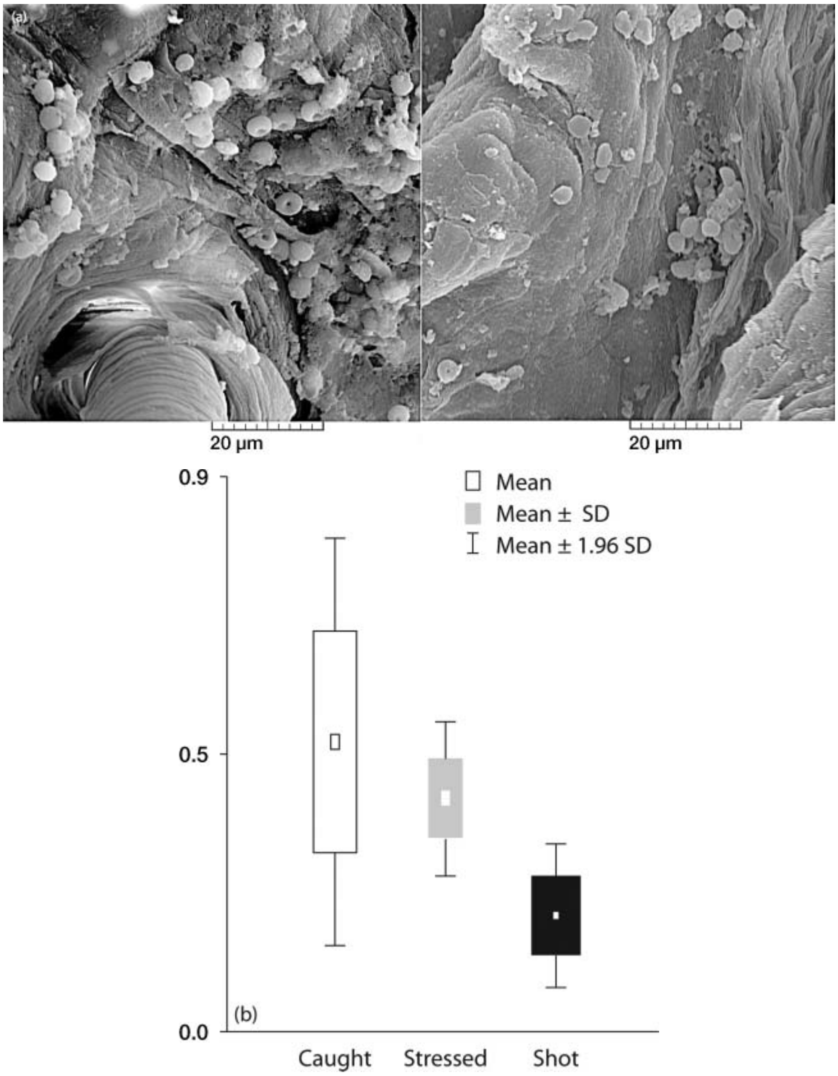

Fig. 3. (a) Microorganisms of brown hare detected at the nose (from the collection of Prof. Naumova). (b) Skin microflora of caught ($n = 39$), shot ($n = 22$), and stressed ($n = 18$) animals. ■ = shot, □ = caught, ▨ = stressed.

and direction of movement. In field experiments, 14 of 21 dogs tried to touch, lick, and smell the plates with mature cultures of bacteria taken from the brown hare while avoiding the plates without bacteria.

Dogs spent more time sniffing the mature cultures of bacteria (W_i, $P < 0.001$) than the agar plates. The frequency of changes in direction of movement towards ‘bacteria’ was significantly higher than that to agar plates (Student’s *t*-test, $P < 0.05$). Given that a sighthound’s behaviour can change in the presence of the odour of cultured microflora, the olfactory stimulus is sufficient for a change of direction, rhythm, and speed of its movements (Shubkina *et al.*, 2010a, 2012).

It is impossible to determine the relative importance of different senses in the field. We can only affirm that in many cases changes in what dogs are seeing lead to changes in their pursuit. But often we see a dog attending to olfactory stimuli by sniffing in a characteristic way. In fact, changes in olfactory stimuli can also lead to changes in the behaviour of sighthounds. Human observers can observe and record the visual but not the olfactory stimuli. However, such behaviour can be recorded photographically (Fig. 4b) and by GPS-tracking (Fig. 4a).

The study of sighthounds hunting hares has shown that their maximal speed, length and duration of pursuit do not determine their hunting success (Shubkina *et al.*, 2008, 2010a, 2010b, 2012). Hunting success is not a direct result of pursuit speed. A comparison of maximal speed distribution in successful and non-successful hunts reveals (Fig. 5) that similar hunting

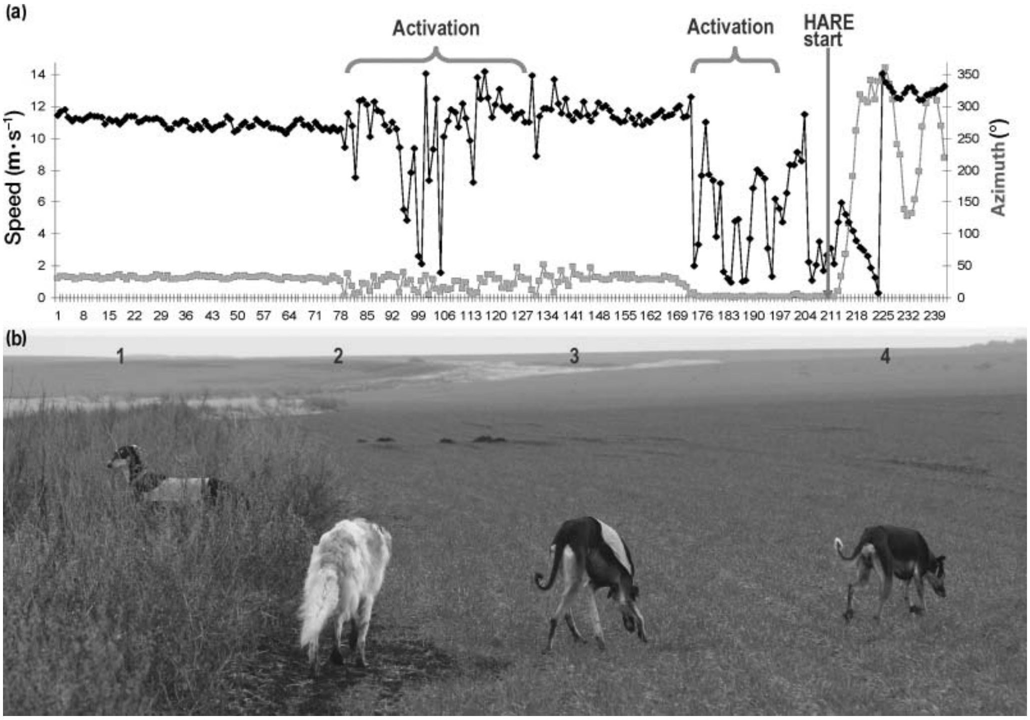

Fig. 4. Sighthound search: (a) example of the initiation of a hare hunt. At first, the dog is on a leash while the hare hides in the grass. The dog and its trainer move together in the open. The grey line represents speed and the black line the azimuth of the dog. The hare bolts at around 211 seconds and the dog is allowed to chase it. But we can detect activation of the dog's search twice before 211 seconds, i.e. at approximately 100 seconds and again at around 169 seconds. Although undetected by the humans involved, the dog must have received some signal that activated its search behaviour (smelling, moving, changing direction). The signal cannot be visual because of the dense grass, and it cannot be aural because the wind rustling the grass will mask the breathing of the hidden hare. It is thus likely olfactory, i.e. the smell of the hare. (b) Four sighthounds searching for their quarry. The one on the far left indeed searches by sight as the name sighthound suggests. But the other three dogs are tracking by scent. Scent-tracking takes place long (~100 s) before the hare comes into sight. So the group name 'sighthound' should not be taken to mean that these dogs are limited to visual information only. They use all their senses but olfactory information in particular is important not only for searching, but also while chasing their prey.

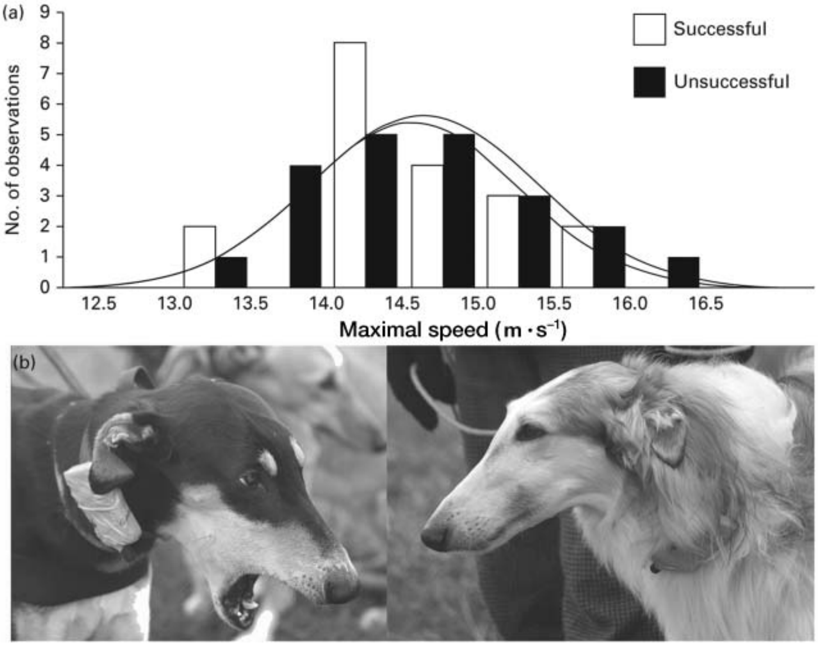

Fig. 5. GPS tracking: (a) upper speed limit and hunting success; (b) dogs with tracking device attached.

success is achieved over the entire speed range (Severtsov and Shubkina, 2014a, 2014b, 2015). These data are consistent with the study of hunting by cheetahs using GPS-tracking (Wilson *et al.*, 2013).

Hunting success (as the relative share of the amount of catches to pursuits) of windhounds is comparatively low – approximately 27% for antelopes and 12% for hares (Shubkina *et al.*, 2010b; Severtsov and Shubkina, 2014a, 2014b, 2015).

DISCUSSION

We have shown that sighthounds, our model predators, selectively eliminate individual prey whose internal organs show abnormalities. Humans, on the other hand, cannot discern these animals by sight, size, gender, age, exterior features or parameters of motion.

Individual brown hare that become prey also have higher concentrations of skin microbiota, which alters their odour compared with other prey. Thus sighthounds can use their sense of smell to help target prey in poor condition.

The amount of skin microbiota is regulated via mechanisms of the generalized adaptation syndrome (Selye, 1978) – a long-term stress reaction. Therefore, elimination of animals with high amounts of microbiota means predators are selecting for stress-resistance in the prey population and are detecting the decreased fitness of particular animals. The concentration of skin microbiota does not determine fitness directly, but indirectly, because it indicates an individual's welfare and prospects of surviving a hunt. Similarly, any direct measurement of stress does not determine fitness directly.

Elimination of animals whose fitness is insufficient to avoid capture means maintaining a population norm of fitness. From this perspective, selection by the predator is a purifying selection, similar to selection leading to the elimination of harmful mutations at the genetic level. Thus, predators resemble human breeders who eliminate a wide range of deviations from a desired phenotype. The high selectivity of elimination by predators is combined with a low success of attack, thereby supporting its control of most of the prey population.

In addition to the odour of the prey, hounds can discriminate prey by sight during pursuit. Yet hunting efficiency is not very high. Hunting success is well below 100% and even below 50%. Underlying such results is the fact that dissemination of odour has a fractal nature influenced by many factors. And the result of the hunt has a multifactorial nature, because it depends upon more than the physical parameters of prey and predator. That is why successful hunting depends on multiple attempts of hunt and pursuit. But this low hunting success of the predator does an efficient job of eliminating specimens with low fitness, regardless of the reason. And so the predator provides stabilizing selection of its prey, substantially influencing that population's quality.

Wild predators – big felids and canids – have hunting efficiencies not dissimilar to those of the hounds. Their success in catching herbivores is rarely more than 50%. Usually it is less, although it is often very high when predators hunt as a group. Its reliable calculation is based on exact estimation of all hunting attempts and thus is limited in field research.

The sighthounds' GPS-data showed that the maximal speed, length and duration of the hunt do not determine whether the hunt is successful. Nonetheless, sighthounds usually hunt by chasing running prey in the open. Such a method of hunting would not be possible unless their speed is comparable to the speed of their quarry. It follows that during the pursuit, sighthounds must be matching the escape attempts of the prey. And so the popular belief – that hunting success of sighthounds is proportional to their speed – cannot be confirmed (Shubkina, 2016).

A windhound's hunt precludes a preliminary assessment of prey availability. It cannot engage in an exploratory survey of prey quality. Hence, windhounds must choose a target animal after beginning the pursuit, the critical time when they must focus on prey selection. That's why they are not particularly successful hunters. However, our results show that the windhound's prey include a higher proportion of animals in poorer health compared with those shot by human hunters (Figs. 2, 3).

We do not believe that future experiments can be accomplished with undomesticated predators in the field. Modern methods of GPS-registration do allow one to count the kill rate relative to numbers of predators or prey, or over some period of time (Zimmerman *et al.*, 2015). But GPS methods do not allow identification of all hunting attempts and their results. Furthermore, at each stage of hunting behaviour there is a trade-off between hunting demand and the prospects of its successful completion. The outcome depends on the predator's motivation, prey properties, and real conditions. A hunt could be terminated by a predator at different stages – while tracking or in preliminary observation, while scaring or chasing, and even after the start of an attack (Mech, 1970; Bologov, 1980, 1981; Filonov, 1989; Aje Uola-Ajan, 2005; Nelson and Mech, 2006; MacNulty *et al.*, 2007).

The future study of wild prey is also problematic. The properties of prey are unknown except for those that can be detected in remains, usually carcasses. The study of bone marrow fat showed that animals that were preyed upon were different from the animals that died because of other reasons (Cheatum, 1949, cited in Franzmann and Arneson, 1976; Greer, 1968, cited in Mech and Delgiudice, 1985; O'Gara and Harris, 1988; Okarma, 1991; Sinclair and Arcese, 1995; Mduma *et al.*, 1999; Pole *et al.*, 2004; Mech, 2007). But such studies do not explain the reason for the difference or the connections with the quality of the prey population. To understand the main principles of predator–prey interactions and their ecological and evolutionary results, we must be able to relate prey features to prey fates.

The experimental study of predator–prey interactions reveals the existence of a tell-tale indicator of the more unfortunate animals, i.e. the enhanced growth of normal microflora on their body surface, a condition that leads to strong odour. And it is this odour that is the previously unknown mechanism for detecting the more vulnerable prey. Perhaps it is one of the most ancient bases of current predator–prey interactions.

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REFERENCES

Aje Uola-Ajan. 2005. The features of wolf–ungulates interactions. In *Proceedings of the Conference on Protection and Management of Animal and Plant Resources*, Irkutsk, pp. 184–189.

Akmaev, I.G. and Grinevich, V.V. 2001. From neuroendocrinology to neuroimmunoendocrinology. *Bull. Exp. Biol. Med.*, **131**: 15–23.

Alexander, E.H. and Hudson, M.C. 2001. Factors influencing the internalization of *Staphylococcus aureus* and impacts on the course of infections in humans. *Appl. Microbiol. Biotechnol.*, **56**: 361–366.

Bailey, M.T., Engler, H. and Sheridan, J.F. 2006. Stress induces the translocation of cutaneous and gastrointestinal microflora to secondary lymphoid organs of C57BL/6 mice. *J. Neuroimmunol.*, **171**: 29–37.

Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R. and Watson, E.G.R. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecol. Appl.*, **16**: 273–284.

Beringer, J., Hansen, L.P., Wilding, W., Fischer, J. and Sheriff, S.L. 1996. Factors affecting capture myopathy in white-tailed deer. *J. Wildl. Manage.*, **60**: 373–380.

Blohina, T.V. 2016. Comparative description of the conditions of European brown hares extracted by two methods. In *Proceedings of the International Conference on Habitats and Fauna of Hunting Animals of Russia*, Rossiysky Agrarian Correspondence University (RGAZU), Balashikha, pp. 34–41.

Bologov, V.P. 1980. Wolf behavior in attacks on domestic animals and prevention of damage to livestock, in *Wolf Behavior: Selected Works*. Moscow: A.N. Severtsov Institute of Ecology and Evolution, Academy of Science of the USSR, pp. 147–156.

Bologov, V.P. 1981. Wolf and herd. *Hunt and Hunting Industry* (*Ohota a ohotnichye hozyastvo*), **3**: 12–13.

Boonstra, R. and Singleton, G. 1999. Population declines in the snowshoe hare and the role of stress. *Gen. Comp. Endocrinol.*, **91**: 126–143.

Boonstra, R., Takagi, N., Bissoon, N., Vij, S. and Gurd, J.W. 2002. Trapping-induced changes in expression of the *N*-methyl-^{d}-aspartate receptor in the hippocampus of snowshoe hares. *Neurosci. Lett.*, **324**: 173–176.

Cheatum, R.L. 1949. Bone marrow as an index of malnutrition in deer. *NY State Conservationist*, **3**: 19–22.

Chitwood, M.C., DePerno, C.S., Flowers, J.R. and Kennedy-Stoskopf, S. 2013. Physiological condition of female white-tailed deer in a nutrient-deficient habitat type. *Southeast. Nat.*, **12**: 307–316.

Choi, E.H., Brown, B.E., Crumrine, D., Chang, S., Man, M.Q., Elias, P.M. *et al.* 2005. Mechanisms by which psychologic stress alters cutaneous permeability barrier homeostasis and stratum corneum integrity. *J. Invest. Dermatol.*, **124**: 587–595.

Davidson, G.A., Johnson, B.K., Noyes, J.H., Dick, B.L. and Wisdom, M.J. 2012. Effect of archer density on elk pregnancy rates and conception dates. *J. Wildl. Manage.*, **76**: 1676–1685.

De Kloet, R. 2000. Stress in the brain. *Eur. J. Pharmacol.*, **405**: 187–198.

DeNicola, A.J. and Swihart, R.K. 1997. Capture-induced stress in white-tailed deer. *Wildl. Soc. Bull.*, **25**: 500–503.

Erofeeva, E.V. 2015. *A non-invasive method of comparing animals' welfare using the sighthounds of native breeds*. Graduation thesis, Moscow.

Erofeeva, E.V. 2016. A non-invasive method of comparing animals' welfare. In *Proceedings of the International Conference on Habitats and Fauna of Hunting Animals of Russia*, Rossiysky Agrarian Correspondence University (RGAZU), Balashikha, pp. 152–161.

Ezenwa, V.O., Jolles, A.E. and O'Brien M.P. 2009. A reliable body condition scoring technique for estimating condition in African buffalo. *Afr. J. Ecol.*, **47**: 476–481.

Fischbach, M. and Bromley, P. 2001. Recombinant cell lines for stress reporter assays. *Cell Biol. Toxicol.*, **17**: 335–351.

Franzmann, A.W. and Arneson, P.D. 1976. Marrow fat in Alaskan moose femurs in relation to mortality factors. *J. Wildl. Manage.*, **40**: 336–339.

Geist, V. 1986. New evidence of high frequency of antler wounding in cervids. *Can. J. Zool.*, **64**: 380–384.

Grandin, T. 1997. Assessment of stress during handling and transport. *J. Anim. Sci.*, **75**: 249–257.

Greer, K.R. 1968. A compression method indicates fat content of elk (Wapiti) femur marrows. *J. Wildl. Manage.*, **32**: 747–751.

Filonov, 1989. *Ungulates and Big Predators in Protected Areas*. Moscow: Nauka.

Hentschel, U., Steinert, M. and Hacker, J. 2000. Common molecular mechanisms of symbiosis and pathogenesis. *Trends Microbiol.*, **8**: 226–231.

Holand, Ø. 1992. Fat indices versus ingesta-free body fat in European roe deer. *J. Wildl. Manage.*, **56**: 241–245.

Krokan, H.E., Kavli, B. and Slupphaug G. 2004. Novel aspects of macromolecular repair and relationship to human disease. *J. Mol. Med.*, **82**: 280–297.

Lacroix, R., Mukabana, W.R., Gouagna, L.C. and Koella J.C. 2005. Malaria infection increases attractiveness of humans to mosquitoes. *PLoS Biol.*, **3** (9): e298.

Lyte, M. 2004. Microbial endocrinology and infectious disease in the 21st century. *Trends Microbiol.*, **12**: 14–20.

MacNulty, D.R., Mech, L.D. and Smith, D.W. 2007. A proposed ethogram of large–carnivore predatory behavior, exemplified by the wolf. *J. Mammal.*, **88**: 595–605.

Marquez, C., Nadal, R. and Armario, A. 2004. The hypothalamic-pituitary-adrenal and glucose responses to daily repeated immobilisation stress in rats: individual differences. *Neuroscience*, **123**: 601–612.

McEwen, B.S., Biron, C.A., Brunson, K.W., Bulloch, K., Chambers, W.H., Dhabhar, F.S. *et al.* 1997. The role of adrenocorticoids as modulators of immune function in health and disease: neural, endocrine and immune interactions. *Brain Res. Rev.*, **23**: 79–133.

Mduma, S.A.R., Sinclair, A.R.E. and Hilborn R. 1999. Food regulates the Serengeti wildebeest: a 40-year record. *J. Anim. Ecol.*, **68**: 1101–1122.

Mech, L.D. 1970. The Wolf: *The Behavior and Ecology of an Endangered Species*. New York: Natural History Press.

Mech, L.D. 2007. Femur-marrow fat of white-tailed deer fawns killed by wolves. *J. Wildl. Manage.*, **71**: 920–923.

Mech, L.D. and Delgiudice, G.D. 1985. Limitations of the marrow-fat technique as an indicator of body condition. *Wildl. Soc. Bull.*, **13**: 204–206.

Millán, J. and Casanova, J.C. 2009. High prevalence of helminth parasites in feral cats in Majorca Island (Spain). *Parasitol. Res.*, **106**: 183–188.

Nelson, X.J. and Jackson, R.R. 2006. A predator from East Africa that chooses malaria vectors as preferred prey. *PLoS One*, **1** (1): e132.

Nelson, M.E. and Mech, L.D. 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. *Am. Midl. Nat.*, **155**: 373–382.

O'Gara, B. and Harris, R. 1988. Age and conditions of deer killed by predators and automobiles. *J. Wildl. Manage.*, **52**: 316–320.

Okarma, H. 1991. Marrow fat-content, sex and age of red deer killed by wolves in winter in the Carpathian mountains. *Holarctic Ecol.*, **14**: 169–172.

Owen-Smith, N. 2016. Mechanisms of coexistence in diverse herbivore–carnivore assemblages: demographic, temporal and spatial heterogeneities affecting prey vulnerability. *Oikos*, **124**: 1417–1426.

Padgett, D.A. and Glaser, R. 2003. How stress influences the immune response. *Trends Immunol.*, **24**: 444–448.

Pepin, D. 1987. Dynamics of a heavily exploited population of brown hare in a large-scale farming area. *J. Appl. Ecol.*, **24**: 725–734.

Pole, A., Gordon, I.J., Gorman, M.L. and MacAskill, M. 2004. Prey selection by African wild dogs (*Lycaon pictus*) in southern Zimbabwe. *J. Zool.*, **262**: 207–215.

Preisser, E.L., Bolnick, D.I. and Benard, M.F. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology*, **86**: 501–509.

Sanders, V.M. and Straub, R.H. 2002. Norepinephrine, the β-adrenergic receptor, and immunity. *Brain Behav. Immun.*, **16**: 290–332.

Santos, J.P., Fernández-de-Mera, I.G., Acevedo, P., Boadella, M., Fierro, Y., Vicente, J. *et al.* 2013. Optimizing the sampling effort to evaluate body condition in ungulates: a case study on red deer. *Ecol. Indicat.*, **30**: 65–71.

Selye, H. 1978. *The Stress of Life*. New York: McGraw-Hill.

Severtsov, A.S. and Shubkina, A.V. 2014a. Predator–prey interaction between individuals: 1. The role of predators in natural selection. *Zoologicheskii Zhurnal*, **93**: 768–777 [published 2015 in *Biol. Bull.*, **42**: 633–642].

Severtsov, A.S. and Shubkina, A.V. 2014b. Predator–prey interaction between individuals: 2. Mechanisms of selection. *Zoologicheskii Zhurnal*, **93**: 1010–1019 [published 2015 in *Biol. Bull.*, **42**: 643–651].

Severtsov, A.S. and Shubkina, A.V. 2015. The evolutionary role of predatory mammals and mechanisms of its realization. *Zhurnal Obshchei Biologii*, **76**: 355–368.

Severtsov, S.A. 1951. On the extinction of animals in the struggle for existence. In *Problems of Animal Ecology*, Vol. 1. Moscow: Akad. Nauk SSSR, pp. 97–136.

Shubkina, A.V. 2006. Analysis of predator response to prey using Borzoi hounds as a model. In *Problemy issledovaniya domashnei sobaki. Materialy soveshchaniya* [*Proceedings of a Conference on the Problems in Studies on Domestic Dogs*], Inst. Probl. Ekol. Evol. Ross. Akad. Nauk, Moscow, pp. 53–67.

Shubkina, A.V. 2016. The hunting success of windhounds. In *Proceedings of the International Conference on Habitats and Fauna of Hunting Animals of Russia*, Rossiysky Agrarian Correspondence University (RGAZU), Balashikha, pp. 539–552.

Shubkina, A. and Ushakova N. 1994. Odors of skin bacteria in prey selection. In *Chemical Signals in Vertebrates VII* (R. Apfelbach, D. Müller-Schwarze, K. Reutter and E. Weiler, eds.), pp. 259–265. Oxford: Pergamon Press.

Shubkina, A.V., Severtsov, A.S. and Chajanov, N.V. 2008. Possible applications of a GPS-based hardware-software complex to characterize animal movements and behavior in the steppe and forest-steppe zones. *Zoologicheskii Zhurnal*, **87**: 1–11.

Shubkina, A.V., Severtsov, A.S. and Chepeleva K.V. 2010a. Study of windhound hunting behavior using GPS-registration: numeral description of search and prey coursing. *Zoologicheskii Zhurnal*, **89**: 1–16.

Shubkina, A.V., Severtsov, A.S. and Chepeleva, K.V. 2010b. Predator and prey: the problem of selective removal at the level of the individual. *Vestnik Okhotovedenia*, **7**: 5–22.

Shubkina, A.V., Severtsov, A.S. and Chepeleva, K.V. 2012. Factors influencing the hunting success of the predator: a model with sighthounds. *Izvestiya Akademii Nauk, Seriya Biologicheskaya*, **1**: 78–90 [published 2012 in *Biol. Bull.*, **39**: 65–76].

Silanikove, N. 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. *Livestock Production Science*, **67**: 1–18.

Sinclair, A.R.E. and Arcese, P. 1995. Population consequences of predation-sensitive foraging – the Serengeti wildebeest. *Ecology*, **76**: 882–891.

Slobodkin, L.B. 1961. *Growth and Regulation of Animal Populations*. New York: Holt, Rinehart & Winston.

Sokolov, V.E., Severtsov, A.S. and Shubkina, A.V. 1990a. Modeling the selective impact of predator on prey: using borzoi hounds to catch the saiga. *Zoologicheskii Zhurnal*, **69**: 117–125.

Sokolov, V.E., Ushakova, N.A., Abramova, O.J. and Shubkina, A.V. 1990b. Responses of microbial associations of skin sites to changes in the physiological state of mammals. *Izvestiya Akademii Nauk, Seriya Biologicheskaya*, **5**: 694–700.

Sokolov, V.E., Ushakova, N.A., Prichodko, V.I., Nekludova, T.I., Gromov, V.S. and Belousova, I.P. 1990c. Specific features of microbial associations in secretions of some mammalian skin glands. *Mikrobiologiya*, **59**: 472–481.

Sokolov, V.E., Ushakova, N.A., Shubkina, A.V. and Nekludova T.I., 1991. Stress as a factor disturbing stability of skin microbial associations. *Doklady Akadameii Nauk SSSR*, **317**: 764–768.

Sokolov, V.E., Ushakova, N.A., Chernova, O.F. *et al.* 1992. Interaction between hair surface and bacteria during changes in the physiological state of mammals. *Doklady Akadameii Nauk SSSR*, **323**: 980–983.

Sokolov V.E., Ushakova N.A. and Chernova O.F. 1993. The interaction between bacteria and the surface of the skin and hair in mammals. *Izvestiya Akademii Nauk, Seriya Biologicheskaya*, **4**: 519–524.

Sokolov, V.E., Ushakova, N.A., Surov, A.V. and Telitsyna A.C. 1994. The participation of vaginal bacteria in *Phodopus campbelli* in the chemical communication between male and female. *Izvestiya Akademii Nauk, Seriya Biologicheskaya*, **5**: 810–817.

Sokolov, V., Shubkina, A. and Bukvareva, E. 2001. *Sobaki mira* (*Dogs of the World*). Moscow: Astrel.

Steinert, M., Hentschel, U. and Hacker, J. 2000. Symbiosis and pathogenesis: evolution of the microbe–host interaction. *Naturwissenschaften*, **87**: 1–11.

Stott, P.G. and Harris F. 2006. Demographics of the European hare (*Lepus europeaus*) in the Mediterranean climate zone of Australia. *Mammal. Biol.*, **71**: 214–226.

Theis, T. and Stahl, U. 2004. Antifungal proteins: targets, mechanisms and prospective applications. *Cell. Mol. Life Sci.*, **61**: 437–455.

Ushakova, N.A. and Shubkina, A.V. 1991. Involvement of mammalian skin bacteria in chemical communication of animals. In *Problemy khimicheskoi kommunikatsii zhivotnykh* [*Problems in Chemical Communication of Animals*], pp. 323–330. Moscow: Nauka.

Valeix, M., Loveridge, A.J., Chamaille-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H. *et al.* 2009. Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. *Ecology*, **90**: 23–30.

Verhulst, N.O., Beijleveld, H., Knols, B.G.J., Takken, W., Schraa, G., Bouwmeester, H.J. *et al.* 2009. Cultured skin microbiota attracts malaria mosquitoes. *Malaria J.*, **8**: 302.

Verhulst, N., Mukabana, W.R., Takken, W. and Smallegange, R. 2011a. Human skin microbiota and their volatiles as odour baits for the malaria mosquito *Anopheles gambiae* ss. *Entomol. Exp. Appl.*, **139**: 170–179.

Verhulst, N.O., Qiu, Y.T., Beijleveld, H., Maliepaard, C., Knights, D., Schulz, S. *et al*. 2011b. Composition of human skin microbiota affects attractiveness to malaria mosquitoes. *PLoS One*, **6** (12): e28991.

Vicente, J., Perez-Rodriguez, L. and Gortazar, C. 2007. Sex, age, spleen size, and kidney fat of red deer relative to infection intensities of the lungworm *Elaphostrongylus cervi*. *Naturwissenschaften*, **94**: 581–587.

Wilson, A.M., Lowe, J.C., Roskilly, K., Hudson, P.E., Golabek, K.A. and McNutt, J.W. 2013. Locomotion dynamics of hunting in wild cheetahs. *Nature*, **498**: 185–189.

Zimmerman, B., Sand, H., Wabakken, P., Liberig, O. and Andreassen, H. 2015. Predator dependent functional response in wolves: from food limitation to surplus killing. *Anim. Ecol.*, **84**: 102–112.

Zwierzina, H. 1999. Biological therapy – where do we stand? *Eur. J. Cancer*, **35** (suppl. 5): SI–S3.