The Natural Chase

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" Wolves awaiting a hunt "

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FOREWORD

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The natural world and the complexity of it and what we do to it is increasingly exposed and under scrutiny through the press, scholarly studies, animal welfare societies and particularly television programmes. This is to be much welcomed as it is only by a thorough understanding of the biology of wildlife communities that one can gain an effective appreciation of the intricacies of their biology as they affect population dynamics and support prey-predator relationships. Essential to this understanding is the role of wildlife as reservoirs of disease for man and his domestic animals.

Thrust into this complexity is the emotive issue of hunting with dogs, but regardless of one's opinion on the issue of hunting, this document brings new evidence which was not available at the time of the Burns Report (2000). As a member of that enquiry I recognised that there were a number of lacunae of essential information from which conclusions on hunting with dogs might have been drawn, much according to the side of the debate one wished to promote, but for which no firm evidence existed.

This document is a scholarly contribution of the factors determining fitness of wildlife populations. It is well researched, referenced and presented: it draws on independent and peer reviewed evidence from several countries and should serve as a valued contribution to wildlife biology.

Lord Soulsby

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Katie Colvile. November 2007.

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1. Purpose.
   The purpose of this review is to explore the concept of the ‘natural chase’. Particular aspects of the predator-prey relationship are reviewed: the ways in which predation influences the behaviour of prey populations; the effects of predators on their wider environment; and factors affecting the success or character of the chase.

2. Background.
   Hunting with hounds has been a focus of contentious debate in the United Kingdom for many years. Following intense pressure from the anti-hunt lobby the government introduced the Hunting Act, which became law in November 2004 and came into force in February 2005. This outlawed the use of packs of dogs to hunt wild mammals, notably foxes, deer, hares and mink (Office of Public Sector Information 2004). In the absence of hunting, however, these species are inevitably controlled by other means such as shooting, trapping and snaring (Burns 2000 and Macdonald et al. 2000). These methods have their own welfare implications. Many people have therefore voiced concern regarding the impact of the hunting ban on the welfare of quarry species (e.g. Fox et al. 2005 and VAWM 2005).

   It is important that the relative merits of hunting and other control methods are reviewed carefully, in order that those in government can be well informed should they consider amending or repealing the Hunting Act in the future. Further, it is pertinent to note that over half of the literature reviewed in this paper was published after the Burns Inquiry of June 2000. The most significant aspect of hunting with hounds, which sets it apart from other methods of population control, is the animal-animal interaction at its heart: a pack of hounds hunting a prey animal. The pursuit of prey by predators is a natural phenomenon: it occurs in the wild in the absence of human intervention. The method by which a pack of hounds hunts is not dissimilar to the method employed by a pack of wolves (see below) and may well be considered ‘natural’. By utilising this natural interaction, hunting with hounds differs crucially from other ‘artificial’ methods of population control.

   In the initial stages of a hunt, hounds find a quarry animal by detecting and following its scent. When the quarry becomes aware of the hounds, it will start to move off. The pace of any pursuit will be dependent on the strength of the scent, but if the hounds catch sight of the quarry their pace will quicken as they attempt to run the animal down. The huntsman’s role in a hunt is to guide the hounds, firstly to where they might pick up the scent of the quarry and, secondly, during the subsequent pursuit phase. Human ‘followers’ of a hunt (whether mounted or on foot) are merely that: they follow the hounds at a distance.

   Genetic studies have confirmed that domestic dogs are descended from wolves (Savolainen et al. 2002, Vilà et al. 1997). It is likely that the two species use similar techniques to hunt prey (Harrington and Asa 2003, Peterson and Ciucci 2003); this view is supported by the species’ close taxonomic relationship and observation of the hunting behaviour of wild wolves. Olfaction (smell) appears to be an important means of prey detection in wolves, as it is in hounds, particularly in forested areas (Harrington and Asa 2003, Peterson 1977, Mech 1966). Once wolves have detected the prey’s scent they will start to stalk it (Peterson and Ciucci 2003). In the case of large prey species, such as deer, elk and moose, wolves rarely attack the prey animal while it remains stationary, instead they wait until it flees before giving chase (Peterson and Ciucci 2003).

3. **Predators play an important role in 'shaping' their environment.**
The important role that predators play within their environment has been recognised increasingly in recent years (e.g. Byrnes et al. 2006, Berger et al. 2001a, McLaren and Peterson 1994, Terborgh 1988). A change in the abundance or distribution of predators may have far-reaching effects on other plant and animal species within their environment.

Herbivores (plant-eaters) are common prey species for carnivores (meat-eaters). Grazing by herbivores suppresses the growth of their food plants, so that changes in herbivore abundance or distribution affect vegetation growth significantly (Byrnes et al. 2006, Berger et al. 2001a). For example, the negative impact of deer on the growth of upland and woodland vegetation in Britain is well recognised and has led to the implementation of population control measures (Milne et al. 1998, Putman and Moore 1998). Herbivore grazing on plant species may impact indirectly on other animal groups: for example, browsing by muntjac deer on honeysuckle in Cambridgeshire woodland caused a decrease in the number of potential egg-laying sites for the White Admiral butterfly (Pollard and Cooke 1994).

Predators tend to affect an ecosystem through their influence on herbivore populations. Predators' effects become evident when they disappear from an ecosystem, since this allows expansion of herbivore (prey) populations (Berger et al. 2001a and Byrnes et al. 2006). Such population expansion may have a number of consequences including increased disease spread within the prey population (Wilson and Childs 1997), an alteration in vegetation cover and decreased species diversity. The indirect effects of predators on vegetation and species diversity have been demonstrated for a variety of different habitats and species (Byrnes et al. 2006). For example, in the Greater Yellowstone Ecosystem in North America extinction of wolves and grizzly bears was associated with an expansion in moose numbers, which led to alterations in vegetation and a related reduction in migrant bird numbers (Berger et al. 2001a). The influences of predators on habitats can also be observed when they are re-introduced into an area. For example, the re-introduction of wolves into Yellowstone in 1995 and 1996 led to improved growth of certain plant species (Ripple and Beschta 2003).

It is likely that predators have many other indirect effects on ecosystems (Mech and Peterson 2003). For example, predators leave prey carcasses that support populations of scavengers (Mech and Peterson 2003).

4. **The presence of predators affects the behaviour of a prey population.**
Predators are known to influence prey species in a number of ways, which include effects on the size and behaviour of prey populations.

4.1. **Prey populations may alter their distribution in response to predation pressure.**
In areas where predation pressure is high, prey animals have been observed to modify their daily behaviour in response to predators (e.g. Hunter and Skinner 1998, Gude et al. 2006). Herbivores become more vigilant in areas where predators are present (Hunter and Skinner 1998, Laundré et al. 2001); accordingly the amount of time they spend feeding may be reduced and they may sacrifice food quality in order to inhabit safer areas (Molvar and Bowyer 1994). Herbivore populations are also more mobile in areas where predation pressure is high (Gude et al. 2006), leading to reduced grazing pressure in these areas. Some prey species are thought to form groups in order to reduce predation risk (Mech and Peterson 2003, Elgar 1989), with individuals on the edges of groups tending to be the most vigilant (Hunter and Skinner 1998).

4.2. **Prey species have evolved many different characteristics in response to predation pressure.**
Predation is likely to have been one of the main pressures for natural selection: certain anatomical features of many prey species have evolved and persisted because they lessen the likelihood of capture by predators (Mech and Peterson 2003, Wirsing 2003, McCollum 1996). In a similar way, the behaviour and life history strategies of many prey species appear to have evolved in response to predation pressure (Mech and Peterson 2003, Harvey and Greenwood 1978).

4.3. **Prey species have been shown to respond to certain predator-related stimuli.**
Certain predator-related stimuli have been found to affect the behaviour of prey animals so that they are less likely to encounter a predator. Cues may involve a number of different senses, such as the odour of predators (Barreto and Macdonald 1999, Smith et al. 1994), or auditory stimuli such as wolf howls (Berger et al. 2001b) and other predator calls (Cheney and Seyfarth 1990).

Prey species are also responsive to the behaviour of scavengers. For example, moose in North America are sensitive to the calls of ravens, which tend to be found in association with moose's predators such as wolves and grizzly bears (Berger 1999). Such 'second-order' associative learning (see below) could explain a wide range of prey behaviour and greatly extend the range of behaviour that can be understood without invoking conscious understanding and analysis on the part of the animal.

The response of prey to predator-related stimuli may either be an innate (instinctive) response that is genetically 'hard wired' (Barreto and Macdonald 1999), or may develop as a result of 'associative learning' (Blumstein 2002, Berger et al. 2001b), whereby an animal learns that a stimulus is associated with a negative experience and exhibits evasive behaviour when it is encountered again. Such learnt or 'acquired' avoidance behaviour can develop after only a few encounters with a predator, such as in female moose that became more sensitive to wolf howls after losing calves to wolves in Yellowstone National Park (Berger et al. 2001b).

Behaviour can be passed down generations in a number of ways (Galef 1976): through inheritance of the genetic basis for a behaviour; through associative learning in successive generations of individuals encountering the same environmental stimuli; or through social interaction of young or naïve animals with experienced ones – 'social learning'. Through this social learning, individuals acquire predator-avoidance or alarm behaviour in response to a predator-related stimulus, after observing conspecifics exhibiting the same behaviour in response to the same stimulus. Animals exhibiting anti-predator behaviour may not, therefore, have had the negative experience of a predator encounter. This social learning is likely to reduce the costs associated with acquired learning (Galef 1976) and has been demonstrated in a range of mammalian and avian species (Griffin 2004, Griffin and Evans 2003). Juvenile rhesus monkeys became fearful of snakes after observing companion animals respond fearfully to snakes (Mineka and Cook 1988), and tammar wallabies acquired vigilance towards a model fox after observing companion animals respond fearfully to the model (Griffin and Evans 2003).

4.4 Anti-predator behaviour may be lost in the absence of predators.

The influence of predator presence on prey behaviour is evident when predators disappear from an ecosystem. Moose in Scandinavia, where wolves were exterminated during the 19th and 20th centuries, showed a different behavioural response to approach by wolves than moose in areas of North America, where wolves are still present (Sand et al. 2006). Scandinavian moose would immediately flee from wolves, whereas North American moose would 'stand at bay'. This behaviour in the latter case resulted in a lower hunting success for North American wolves. Similarly, group sizes of pronghorn (Berger et al. 1983) and musk ox (Heard 1992) were found to be smaller in areas where predators had been absent for at least 25 years, and moose had lost their sensitivity to the calls of ravens in areas where wolves and grizzly bears had been extinct for at least 50 years (Berger 1999).

In other instances, however, anti-predator behaviour may persist despite predator absence for considerably longer periods than in these previous examples (Byers 1998). Behaviours that have no genetic component and are learnt will be lost more quickly from a population than those that have a genetic basis (Blumstein 2002). The absence of all predators is more likely to lead to loss of anti-predator behaviour than the absence of a few predators (Blumstein 2002).

Vigilance levels in some prey species appear to be directly related to predator presence and in such species the absence of natural predators may be associated with reduced vigilance (Wolff and Van Horn 2003, Hunter and Skinner 1998).

4.5. Prey populations may regain their anti-predator behaviour when predators are re-introduced to an area.

The effect of predators on prey behaviour is also demonstrated when predators are re-introduced in an area. Anti-predator behaviour in prey species such as elk (Laundré et al. 2001) and impala (Hunter and Skinner 1998) was found to be significantly greater in areas where carnivores had been re-introduced than in areas where they were absent. Anti-predator behaviour has also been shown to increase over time in prey populations, as predators re-colonise an area. For example, the vigilance of elk increased steadily over 5 years as wolves re-colonised Yellowstone National Park (Laundré et al. 2001) and the hunting success of bears in Scandinavia was highest for animals on the 'expansion front' (Berger et al. 2001b), suggesting that prey were learning to modify their behaviour in response to their encounters with bears. These behavioural changes are likely to occur as a result of associative learning and may therefore return in as short a period of time as one generation (Laundré et al. 2001, Berger et al. 2001b).

However, disappearance of 'hard-wired' anti-predator behaviours may leave a population vulnerable if predators return in the future. For example, Scandinavian moose have yet to alter their behaviour since wolf re-colonisation of the Scandinavian peninsular in the late 1980s, with the result that they are predated on more successfully than their genetically wiser counterparts in North America (Sand et al. 2006).

4.6 Prey may alter their behaviour towards humans if human persecution which Replaces predation by animal predators.

In the same way that prey alter their behaviour in response to predators, so their behaviour can change in response to human persecution, which may select for different aversive behaviour than that resulting from predation by animal predators (Sand et al. 2006). Scandinavian moose are persecuted by humans significantly more than moose in North America and are considerably less aggressive towards humans than their North American counterparts: Scandinavian moose will flee from people whereas North American moose are more likely to stand their ground (Sand et al. 2006). Scandinavian moose will also flee from wolves, but this is a less effective strategy (against wolves) than standing their ground. Therefore, persecution by human shooters appears to have selected for behaviour that is less effective against wolf predators (Sand et al. 2006). Despite continued persecution by humans, it appears that the absence of wolves for generations has allowed Scandinavian moose to lose their effective anti-wolf behaviour.

5. Predation pressure retains the 'fitness' of a prey population.

Preceding examples have illustrated how predator presence may positively influence the evolutionary fitness of prey. Namely, predators can make a prey population more vigilant, so that individuals and groups are better able to cope with predation and other threats. In areas where predators have disappeared from an ecosystem there is a risk that prey will not regain effective anti-predator behaviour, should predators return or be introduced (as in the Scandinavian moose example).

Predators have also been shown to keep prey populations healthy. In ecosystems where predators suppress prey numbers, removal of predators leads to expansion of prey populations, which can lead to increased disease spread between individuals (Wilson and Childs 1997). In addition, predators selectively cull weaker animals: old (Evans et al. 2006, Pierce et al. 2000, Kunkel et al. 1999, Mech et al. 2003), young (Kunkel et al. 1999) or diseased individuals (Packer et al. 2003, Mech et al. 2003, Murray et al. 1997). By culling old and diseased individuals predators maintain a healthier prey population (Mech and Peterson 2003). Predators have been shown to selectively remove prey with high parasite burdens (Packer et al. 2003, Mech et al. 2003) and in such cases paradoxical effects on prey numbers may be observed: when predators are removed, prey numbers may decrease due to increased disease incidence within the population (Packer et al. 2003). This selection of weaker animals probably occurs because individuals in suboptimal health are less able to outrun predators than healthy individuals (Mech and Peterson 2003). Wolves have also been observed to 'home in' on weaker individuals within a herd prior to the chase (Mech and Peterson 2003).

6. Many natural factors influence hunting success.

The predator-prey interaction is a complex one, as this review has already demonstrated. The interaction becomes more complex when one considers the many factors that may influence the hunting success of predators. These may be prey-related, predator-related or environmental factors. Because many factors can influence hunting success there is wide variation in predator kill rates, both within and between predator-prey groups. For example, seven variables were found to affect hunting success in lions (Funston et al. 2001), leading to variable kill rates, and wolf-moose kill rates varied tenfold amongst populations in North America (Messier 1994).

The factors affecting hunting success in carnivores are discussed below. The hunting techniques of predators vary, so that different variables are important for different species (Murray et al. 1995).

6.1. Prey factors.

The density of prey populations considerably influences predator kill rates. In North America the population density of moose was the most important influence on wolf-moose kill rates (Messier 1994), and the density of primate prey was the most significant factor affecting the level of predation by forest leopards (Züberbuhler and Jenny 2002).

The species of prey being hunted has been shown to affect the hunting success of lions (Funston et al. 2001). The age and sex structure of the prey population can also be important: the most vulnerable animals in a prey population are hunted preferentially and more successfully. For example, wolves and cougars hunt young or old animals most frequently (Mech and Peterson 2003, Kunkel et al. 1999). Female mountain lions with offspring selected female adult deer more often than would be expected by chance (Pierce et al. 2000). In addition, prey group size has been shown to affect lions' hunting success (Funston et al. 2001).

6.2. Predator factors.

Wolves, wild dogs and lions are examples of large carnivore predators that hunt in packs. In these species, group size has been shown to influence hunting success, as well as the length of the chase and the size of prey killed.

A pack size over a certain threshold has been demonstrated to improve hunting success for both lions (Funston et al. 2001) and wild dogs (Creel and Creel 1995, Fanshawe and Fitzgibbon 1993). Larger pack size has also been shown to enable wild dogs to defend carcasses against other predators (spotted hyaenas) more successfully (Fanshawe and Fitzgibbon 1993).

In relation to wild dogs, shorter chase distances were observed for packs with a higher number of adults (Creel and Creel 1995). Food intake per dog per kilometre chased was found to be greatest with a pack size of between five and 14 adults and this matched observed pack sizes.

An association between pack size and prey size has been demonstrated for spotted hyaena (Kruuk 1972), wolves (Mech 1970) and African wild dogs (Fanshawe and Fitsgibbon 1993), although the relationship is not universal and larger pack size could be a cause or effect of hunting large prey.

The age and sex structure of a predator population have also been shown to influence hunting success. The hunting success of hyaenas improves as both males and females increase in age (Holekamp et al. 1997). Sex differences in prey selection have been observed for lions (Funston et al. 2001, Funston et al. 1998): male lions tend to hunt larger prey species than females, and will assist in the chase if their pride is hunting large prey such as buffalo (Funston et al. 2001).

6.3. Environmental factors.

Environmental factors also influence hunting success and the length of the chase. Season and climate can be significant factors: up to 15 per cent of variation in wolf kill rates on Isle Royale, Alaska, was explained by inter annual variation in winter climate (Vucetich et al. 2002). Snowy conditions are particularly important with respect to wolf hunts (Mech and Peterson 2003, Mech et al. 2003): increased snow depth decreases chase distances because prey are less able to escape in snowy conditions (Nelson and Mech 1986).

Habitat type can also be important as it affects predator concealment, the ability of predators to chase prey and the ability of prey to flee from predators (Murray et al. 1995). It also affects the type of prey species present and their density (Funston et al. 1998). For example, hunting success in lions was influenced by grass height (Funston et al. 2001), and coyotes hunted more successfully in dense forest than in sparse forest, with shorter chase distances (Murray et al. 1995).

7. Origins of human hunting with dogs.
   There is evidence of the importance of meat in the diets of our human ancestors (Richards 2002). However, the way in which meat was obtained - the relative importance of hunting versus scavenging - has been the subject of some debate (Dominguez-Rodrigo 2002). Current evidence suggests that wolves (dogs' ancestors) were the first species to be domesticated by humans around 15,000 years ago (Davis and Valla 1978). Fiedel (2005) suggested they were useful to humans because of their hunting ability and that their domestication led to a shift in human hunting strategy.

8. *Conclusions and implications for the hunting debate.*
   This review has demonstrated the key role that predators play in regulating the size, health and behaviour of prey populations and the further effects that this has on the ecosystem, particularly on biodiversity. Numerous natural variables have also been demonstrated to influence the interaction between predators and prey.

   It can be seen that there are great similarities between the hunting strategies used by wolves and hounds, with the result that hunting with hounds can indeed be considered a 'natural' method of population control (Section 2). Observation of predator-prey relations in wild animals can therefore be used to make viable inferences regarding the impact of hunting with dogs on wild prey populations and the environment. Such as:

   • The main quarry species (foxes, deer, hare and mink) will adapt their behaviour on a daily basis in order to avoid predation. For example, they will avoid daytime feeding which, in turn, will reduce predation by foxes on the increasingly favoured free-range farming systems in which animals are in the open by day and enclosed by night.

   • Hunting causes quarry species to disperse. Dispersal reduces the impact of quarry species on domestic prey in a particular area (foxes and mink) and reduces their impact on vegetation (deer and hares) (Sections 3 & 4.1).

   • It has been seen (Section 4) that avoidance behaviour may be exhibited by quarry that have not experienced a hunt before. Many such behaviours are innate (hard-wired), having evolved in quarry species in response to threats analogous to that of predation by hounds Section 4.3). Others come as a result of social learning. Yet other predator avoidance behaviour appears to be learnt by experience but it is learnt quickly, perhaps after only a single encounter. As a result of all this, quarry will have a set of methods for coping and so will not be bewildered or panicked by the experience of being hunted. Furthermore, they will rapidly return to their previous behaviour on escape.

   • It has become apparent that rural foxes that are hunted by hounds will avoid humans, while the non-hunted urban foxes have become bold scavenging animals that have lost their instinctive fear of man. This absence of predation pressure may have lead to a less vigilant population in general, so leaving it more susceptible to other threats.

   • In the absence of hunting, avoidance behaviours may be lost from quarry populations (Sections 4.4 to 4.6). This is particularly likely in foxes and deer which now have no natural predators in Britain. Artificial control methods, such as shooting, do not have the same influences on behaviour as natural predation and so will not serve to maintain the same set of behaviours (Section 4.6) .

- *Were hunting to be re-introduced within a few years, it is likely that prey would re-adapt quickly to the threat of predation. On the other hand, if hunting were not re-instated until the distant future, quarry may not be able to regain their genetically based anti-predator behaviour. This would be detrimental to prey if another predator, such as the wolf, was re-introduced (Section 4.5).*

- *Hunting with hounds is likely to have a positive influence on the health of quarry populations since, by its very nature, injured and diseased animals will be selectively culled (Section 5). A full pack of hounds is necessary to maximise successful location in all situations.*

- *Low-density quarry populations are protected when hunting with hounds is used as the method of population control, because hunting is self-limiting in that it spends less time in areas with fewer prey animals. This is not the case with other control methods, such as trapping and poisoning, which could readily be used until the last animal is killed.*

- *The inverse correlation (Section 6.2) between pack size and pursuit time has implications for hunting with hounds. The law now restricts 'pack size' to two dogs; as a result flush/chase distances are likely to be longer and, more importantly, less effective than with a larger pack.*

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