Animal Behaviour xxx (2016) 1–13

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Conservation Behaviour

Animal behaviour and its role in carnivore conservation: examples of seven deadly threats

David W. Macdonald*

Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford, U.K.

ARTICLE INFO

Article history:
Received 16 October 2015
Initial acceptance 11 November 2015
Final acceptance 26 April 2016
Available online xxx
MS. number: SI-15-00889R

Keywords:
carnivore conservation
climate change
disease
guild structure disruption
habitat loss
hunting perturbation
interspecies conflict
invasive species

Habitat loss, climate change, hunting perturbation, disease, invasive species, guild structure disruption and conflict are seven widespread threats to wildlife conservation, with the Carnivora standing at the apex of risk. Fundamental to all of these is the ability of organisms and ecosystems to adapt, else succumb, and it is the extent to which their behaviour is flexible and adaptable that may stand between viability and extinction. Knowledge gained through undertaking original research on aspects of fundamental biology and behaviour assists practitioners and policy makers in the management of conservation problems. Selecting examples of these seven threats from our projects at the Wildlife Conservation Research Unit (WildCRU), I identify the conservation issue concerned, and then explore the behavioural component and its relevance to mitigating that conservation issue. Social systems, demography, life histories, habitat selection, foraging and patch choice, the Allee effect, conspecific attraction, movement, ranging and dispersal are pervasive behavioural elements common across various conservation issues that determine why some populations decline and what can be done to remedy the situation. However, the overarching principle remains the same: effective action requires an understanding of the behaviour of the species concerned. Conservation is most exciting and most difficult at two ends of a continuum: the earthiness of animal lives, human livelihoods and practical action, and the erudition of big ideas, from individual behaviours to the consequences for populations and, ultimately, geopolitical decisions about how humans are to live alongside nature with the wellbeing of both as goals.

In 1485, Netherlandish painter Hieronymus Bosch depicted the Seven Deadly Sins (wrath, envy, avarice, gluttony, idleness, lust and pride), overlooked by a vigilant all-seeing eye: *Cave Cave Deus Videt* ('Beware, Beware, God Sees'). Five hundred years on and the religious iconography of this work maintains a contemporary relevance to our destructive attitudes toward the natural world. Indeed, we may reflect nervously on which of Bosch's 'Four Last Things' – death, judgment, hell or glory – are, metaphorically, the more likely fates for humanity. While the conservationist would refashion these Seven Deadly Threats or Risk Factors, perhaps as habitat loss, climate change, hunting perturbation, disease management, invasive/introduced species, conflict and guild structure disruption, fundamental to all of these is the ability of organisms and ecosystems to adapt, else succumb. And deprived of the luxury of millennia of evolutionary adaptation, for those charismatic megafauna so often the vanguards of public appreciation of nature (Macdonald, Burnham, et al., 2015; Macdonald, Collins, & Wrangham, 2007), it is the extent to which their behaviour is flexible and adaptable that may stand between viability and extinction.

At the apex of risks perch the Carnivora, dependent upon sufficient productivity making it through the trophic chain to sustain them, relying upon extensive ranges, susceptible to habitat fragmentation and loss, vulnerable to a diversity of prey-derived parasites and diseases, bioaccumulators of toxins, hunted for sport and, inevitably, the victims of much human–wildlife conflict (Macdonald, Loveridge, & Rabinowitz, 2010).

One part of the solution to these 'deadly risk factors' requires changing societal attitudes that lead to unsustainable exploitation of natural resources, addressing humanity's disregard for the implications that development can have on wildlife, and refining our often harsh and thoughtless responses to human–wildlife conflicts (Macdonald & Willis, 2013). The second part, however, pertains to understanding better the behaviour of the species involved, enabling practitioners and policy makers to apply knowledge gained through undertaking original research on aspects of

* Correspondence: D. W. Macdonald, Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, The Recanati-Kaplan Centre, Tubney, Abingdon, Oxfordshire, Oxford, OX13 5QL, U.K.

E-mail address: david.macdonald@zoo.ox.ac.uk.

http://dx.doi.org/10.1016/j.anbehav.2016.06.013
0003-3472/

Please cite this article in press as: Macdonald, D. W., Animal behaviour and its role in carnivore conservation: examples of seven deadly threats, Animal Behaviour (2016), http://dx.doi.org/10.1016/j.anbehav.2016.06.013

fundamental biology and behaviour to the management of conservation problems.

The applied discipline of conservation biology (Soule, 1985) has, despite the abundant expression of good intentions, not been fast to engage interdisciplinarity between camps (Macdonald, Loveridge, et al., 2010), although innovative thinkers strive to break the mould (e.g. Mermet, Homewood, Dobson, & Bille, 2013). Conservation biology originally combined the principles of ecology, population biology and genetics to study how populations and their habitats respond to anthropogenic change, and sought to apply this knowledge through protection, restoration and political leverage (Caro, 2007). Indeed, even more than a quarter century ago, various authors lamented the lack of engagement between studies of animal behaviour and conservation biology (e.g. Caro, 1999; Sutherland, 1998). As Caro and Durant (1985) pointed out, those who conduct research can sometimes see conservation practice as second rate, or uninteresting, while conservationists may view pure ecological research as irrelevant or esoteric. This reminds us of the always fallacious divide imagined in the 1960s between ‘pure’ and ‘applied’ research, about which I have remarked that while it is quite difficult to be interesting, it is a lot harder to be useful. Bridging the divide between research-oriented and conservation-oriented objectives is, however, crucial (Macdonald, 2001). Although this ‘call to arms’, for example by Caro (2007), and the multipoint approaches proposed for integrating these subjects sparked a greater level of engagement and interdisciplinarity, demonstrable benefits from applying knowledge of animal behaviour to conservation issues have sometimes proven elusive.

Selecting examples from our projects at the Wildlife Conservation Research Unit (WildCRU) using behavioural ecology to inform conservation, my aim in this paper is to illustrate that knowledge of how a species behaves can be pivotal to its management. Indeed, understanding animal behaviour can be fundamental to understanding, and often to mitigating, each of the seven deadly risk factors. For each, I identify the conservation issue concerned, and then explore the behavioural component, and its relevance to mitigating the conservation issue(s).

HABITAT LOSS

Impacts of Fewer Waterholes on Lion Hunting Success and Predation

Conservation issue concerned

In Hwange National Park, Zimbabwe, we found that waterholes (including pumped ones, as rainwater collected in natural depressions dries up) act as service stations, providing prey along the nocturnal routes traversed by lions, *Panthera leo* (Loveridge et al., 2009; Valeix et al., 2010). As waterholes dry up, and with greater conflicts with agriculture over water supply resulting in the exclusion of game species, we observe that it is not simply that fewer sites affect lion food availability directly, but that there is a disproportionate effect on hunting success – a cascade effect of there being fewer, larger home ranges, resulting from more dispersed available waterholes, especially affecting juvenile males. Furthermore, other arid savannah predators that depend on prey congregating at waterholes are affected in similar ways.

Behavioural component

Lions engage in area-restricted search behaviour (Valeix et al., 2010), focusing on waterholes at which they ambush prey and make 40% of their kills (Davidson et al., 2013; Valeix et al., 2009). Herbivores engage in antipredator behaviours in response to the presence of lions, and so the catchability of herbivores decreases as soon as a lion is detected in an area, a process known as a behavioural resource depression (Charnov, Orians, & Hyatt, 1976; Kotler, 1992). As a result, having killed at one waterhole (and thus often given away their presence), lions generally move immediately to the vicinity of another one (Valeix et al., 2011).

Because, to remain effective, hunting effort has to be rotated between waterholes, and a minimum number of waterholes must be secured (Loveridge et al., 2009; Valeix et al., 2010; Valeix, Loveridge, Macdonald, 2012) such that the more dispersed waterholes are, the larger the lionesses' home range (Valeix, Loveridge, Macdonald, 2012). Ultimately this influences lion population abundance, as fewer prides and coalitions can fit in the landscape if home ranges are larger.

In terms of dispersal behaviour, drawing upon GPS data tracking 50 lions over 10 years (Elliot, Cushman, Loveridge, Mtare, & Macdonald, 2014), we found that juvenile dispersing males were far more prone to leave the protected Park area, making them vulnerable to hunting, than were territorial adults. Notably, these dispersing juveniles also selected for different habitats (Elliot, Cushman, Macdonald, & Loveridge, 2014).

Mitigation benefiting from understanding animal behaviour

Clearly, the policy of surface water management in Hwange affects lion (and other carnivore) populations, and can be used as a tool for large carnivore management and conservation. Because of the differences in movement behaviour and resource selection between dispersers and adults, we propose that when designing connectivity strategies for any species, data should be used from the demographic that is most relevant to connectivity, which in the case of lions is dispersing subadult males (Elliot, Cushman, Macdonald, et al., 2014). We are now exploring the best routes for dispersal corridors to assess implications on connectivity and genetic diversity, and testing a range of scenarios modelling the likelihood that particular land use types will be used by lions preferentially. Nevertheless, attempts to maintain connectivity will only be effective if dispersing individuals actually survive to reproduce, a parameter we found to be highly correlated with the age of dispersal – adult male behaviour largely dictates the age of subadult dispersal, which in turn affects their mortality since dispersing young (<31 months of age) leads to death (Elliot, Valeix, Macdonald, & Loveridge, 2014). This is in part due to dispersing male lions potentially being most prone to human–lion conflict (Elliot, Cushman, Macdonald, et al., 2014), which I will elaborate on later.

Human Impacts on Both Prey Abundance and Prey Availability Affect Amur Tiger Hunting Success

Conservation issue concerned

In the late 19th century, Amur tigers, *Panthera tigris altaica*, numbered some 3000 individuals in populations across portions of China, Korea and Russia (Tian et al., 2011). Just 350 survive today residing, almost exclusively, in Far East Russia (Miquelle et al., 1999). This remnant endangered population lives precariously on the edge of extinction (Gilbert et al., 2014). Aside from poaching, the tiger's plight is compounded by competition with local people over wild game, principally red deer, *Cervus elaphus*, wild boar, *Sus scrofa*, and sika deer, *Cervus nippon*, which combined comprise 89% of the tigers' diet (Petrunenko et al., 2015). However, this population is subject to the lowest prey densities of any tiger population globally. As implementation of management actions necessary to conserve Amur tigers is dependent on a detailed understanding of their hunting behaviour, we asked: how does Amur tiger behaviour within the home range respond to the search for perilously low prey densities?

Behavioural component

There are two broad hypotheses explaining the hunting behaviour of carnivores: the prey abundance hypothesis, which predicts