Trends in Ecology & Evolution

CellPress

Review

Ecology of Problem Individuals and the Efficacy of Selective Wildlife Management

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As a result of ecological and social drivers, the management of problems caused by wildlife is becoming more selective, often targeting specific animals. Narrowing the sights of management relies upon the ecology of certain 'problem individuals' and their disproportionate contribution to impacts upon human interests. We assess the ecological evidence for problem individuals and confirm that some individuals or classes can be both disproportionately responsible and more likely to reoffend. The benefits of management can sometimes be short-lived, and selective management can affect tolerance of wildlife for better or worse, but, when effectively targeted, selective management can bring benefits by mitigating impact and conflict, often in a more socially acceptable way.

Trends

In response to ecological and social drivers, there is a trend towards selective wildlife management that targets the individual rather than the population.

The move towards selectivity in wildlife management is running in parallel with growing recognition of the prevalence and importance of intraspecific variation in ecology and evolution.

As well as being logistically challenging, removing 'problem individuals' may inadvertently apply selective pressures on correlated traits (such as sex, size, or social position) that could have indirect, negative impacts on populations.

Social perspectives on ecological outcomes of selective management highlight the importance of interdisciplinary research integrating ecological and social dynamics.

Current Challenges in Wildlife Management

Predators, large herbivores, and 'pest' species are often managed to mitigate their negative impacts upon human livelihoods and well-being, and upon conservation objectives [1]. This management can be controversial, particularly when the targeted species are charismatic or are themselves of conservation concern. Strategies that attempt to mitigate human-wildlife impacts (see Glossary) can therefore be challenging to develop and implement because effective management requires an understanding of both the ecology of the problem [2], the animals causing it, and its wider social context [1]. Allowing actual or perceived impacts to go unmanaged could result not only in ongoing or escalating social or political pressures [3] but might also lead to increased animosity towards conservation objectives [4], and perhaps to the illegal killing of wildlife [5]. Currently the predominant approach to reducing **human–wildlife impact** (see Glossary) tends to be pro-active or generalised culling [6,7]. There can be advantages to this approach, particularly where routine harvesting or hunting effort can be harnessed [8–10]. Benefits can arise in terms of economic and social gains [8], and reduction of impacts [11], potentially by reducing population size or effecting behavioural change. Such generalised approaches to controlling impacts can, however, incur high financial costs [6], result in reduced ecosystem function [7], have unforeseen ecological outcomes [12], and give rise to ethical and welfare concerns [13], all of which can challenge societal and political support [14].

In integrating these ecological and social considerations, ecologists and managers are, in some instances, moving away from generalised removal of wild species and towards coexistence [15]. This can include narrowing sights from control at a population level towards targeting individual animals [10,16,17]. Indeed, there have been recent calls for the cessation of all wildlife control methods that are not highly selective [6,18].

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To be effective, this concentration of effort upon specific animals relies upon the ecology of these individuals and their disproportionate contribution to deleterious impacts. In framing this issue for the specific case of large carnivore predation of livestock, Linnell *et al.* [19] identified and evaluated the ecological evidence for 'problem individuals'. This notion of disproportionate contribution is clearly evident beyond livestock predation, and has been applied to 'man-eating' lions [20], food-conditioned bears [21], problem elephants [3,22], and 'rogue' sharks [23], as well as to smaller taxa such as seabirds [24], birds of prey [25], and feral cats [26]. Targeting these problematic animals might be intuitively appealing because it is often the apparent actions of particular individuals, and not those that behave 'normally', that engender hostility among human stakeholders [23,27]. It might also be assumed that concentrating management efforts upon fewer, specific animals could incur reduced ecological, social, ethical, and logistic costs.

We broaden the assumption underlying Linnell *et al.*'s [19] problem individual paradigm – that 'a small proportion of the individuals . . . are responsible for most livestock depredation'. We define the problem individual as 'any individual animal that is responsible for a disproportionately large negative impact on human interests', acknowledging that such interests extend beyond the ecological into matters of health, culture, wellbeing, and economics. We use this definition to examine selective wildlife management, drawing on a diversity of research in ecology, animal behaviour, and wildlife biology. Although we concentrate on lethal control as the most typical form of selective management [10], we also consider non-lethal practices such as translocations or those that seek to change individual behaviour *in situ* (Box 1).

We identify and evaluate five key questions (Figure 1) that are fundamental to determining whether targeting problem individuals is a generally viable management strategy: (i) Can most of the problem be ascribed to few individuals? (ii) Is it possible to accurately identify and target problem individuals? (iii) Does targeting problem individuals mitigate impacts? (iv) Can indirect effects be avoided or minimised? (v) Can targeting individuals help to achieve social objectives?

Box 1. Non-Lethal Alternatives in Problem Individual Management

Translocation. Despite occasional successes [57], translocating problem individuals often fails because of high mortality, animals returning to capture sites, and persistence of problem behaviour in the remaining individuals [16,79]. Indeed, in extreme cases it has resulted in an increase in threats to human safety [3,80]. The translocation of problem leopards in India, for example, is thought to have increased attacks on people [80].

Diversionary Feeding. Targeting subsets of wild animal populations with **diversionary feeding** has shown promise in reducing impacts [81]. In Scotland, for example, Amar *et al.* [82] used habitat data to predict which hen harriers *Circus cyaneus* pairs were likely to have the highest predation rates on red grouse *Lagopus lagopus scoticus* chicks, and they were able to successfully reduce grouse chick predation by providing diversionary food to specific harrier nests. The benefits of diversionary feeding have, however, been reduced by unintentional increases in population sizes and anthropogenic dependency [81].

Aversive Conditioning. Despite some encouraging indications (e.g., shock collars on individual wolves resulted in whole packs developing an aversion to specific baited 'shock zones' [83]), field trials attempting to use **aversive conditioning** to prevent carnivore predation of livestock have so far all failed [84]. However, 'hazing' (a form of aversive conditioning) has proved successful with many nuisance bears around human settlements, particularly for bears that are not already 'food conditioned' [85]. This proactive approach could be targeted either at animals displaying the characteristics of future troublemakers (such as 'bold' personality types in ungulates [86]) or at animals responsible for teaching problem behaviour, such as female bears [33].

Physical Handicapping. This non-lethal method is on the furthest extreme of impact mitigation. In one of the few cases where such an approach was attempted it was remarkably successful: in Kenya the de-tusking of specific 'destructive' bull elephants resulted in their fence-breaking behaviour being reduced by 1.7–14.5-fold and the mean rate of their attack falling sixfold [22].

Glossary

Aversive conditioning: attempting to change the behaviour of individual animals through associations with a negative stimulus introduced during a human–wildlife impact [84].
Conservation conflicts: situations that occur when two or more parties with strongly held opinions clash over conservation objectives and when one party is perceived to assert its interests at the expense of another [1].
Diversionary feeding: the use of food to divert the activity or behaviour of a target species from an action that causes a negative impact, without the intention of increasing the density of the target population [81].
Foraging specialisation: a foraging behaviour consistently expressed by an individual that is uncommon relative to their population.
Human–wildlife impacts: the direct and often negative interaction between humans and wildlife species. Such interactions can lead to conservation conflicts.
Keystone individual: an individual that has a disproportionately large and irreplaceable effect on other group members and/or the overall group dynamics [32].
Personality type: a particular combination of behavioural tendencies that are consistently expressed [99].
Problem animal profiling: using data on previous human–wildlife impacts to identify those demographic classes most likely to have a negative impact (also known as predator profiling) [26].
Problem component: where a specific, negative behaviour continues to be observed within a population despite problem animal removal [59].
Site effect: where variables common to a location result in increased human–wildlife impact [60].

Ecological evidence	Targeting feasibility	Impact evaluation	Refinement	Social assessment
1. Can most of the problem be ascribed to few individuals?	**2. Is it possible to accurately identify and target culprits?**	**3. Will targeting problem individuals or classes mitigate the impact?**	**4. Will there be undesirable indirect effects, can they be avoided or minimised?**	**5. Can targeting individuals help to achieve social objectives?**
Quantify individual variation, specifically role of individual animals in impact [Box 2]. Consider over-representation of particular demographic classes [23,38].	Evaluate accuracy of targeting method (e.g., by applying forensic methods [Box 2] to distinguish problem individuals from conspecifics).	Use treatments such as experimental trials to explore relative effectiveness of non-lethal management *in situ* [Box 1] against removal [64].	Include indirect, additional effects (e.g., behavioural, demographic, social, evolutionary impacts) as outcomes in trials [42]. Particularly in cases of on-going removal.	Assess if method will meet intended social objectives (e.g., increase tolerance toward species [77]). If assessment highlights conservation conflict see [1].

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Figure 1. Evaluating Selective Wildlife Management. A conceptual framework illustrating the recommended stages of selective management (yellow), the questions that determine its viability (blue), and methods to answer them (green). see also [1,23,38,42,64,77] and Boxes 1 and 2.

(i) Can Most of the Problem Be Ascribed to Few Individuals?

Evidence of individuality in wild animals is clearly central to the efficacy of managing problem individuals (Figure 1) but is also fundamental to ecology and evolution. To understand the phenomenon in this context, it is necessary to look at the ultimate and proximate mechanisms that give rise to individual variation [28]. Ultimately, theory suggests that intraspecific variation reduces intraspecific competition [29]. As a result, it might be expected that individual variability is particularly pronounced in species such as ecological generalists [29] or those occupying upper trophic levels [28]. More proximately, intraspecific behavioural variation can stem from a complex combination of genetic variability and phenotypic plasticity. Considering, for example, the ontogeny of a predator's **foraging specialisation**, individual behaviour might be influenced by variables common to local conspecifics such as group size, environmental conditions, prey species identity and abundance, and by individual variables such as **personality type**, size, sex, age, and reproductive status [30,31]. These individual variables will also determine the extent to which a behaviour is consistently or intermittently expressed [32]. Where a behaviour is consistently expressed by an individual there is evidence that it can be passed on to offspring [33] or to associates through social learning [34]. As a consequence of individual variation, animals with access to the same resources can exploit them very differently [28]. This can be observed in diverse taxa through individual variations in risk-taking [35], diet [36], or foraging [37].

Growing awareness of intraspecific behavioural variation has prompted a raft of research exploring how the phenomenon might influence ecological and evolutionary processes, natural and sexual selection [38], ecological invasions [39], and predator–prey dynamics [30]. These studies identify the major roles of within-population variation in community ecology [29]. However, the influence of individual behaviour on how wild animals interact with humans has so far received little attention, despite clear pathways by which it might be important [2]. Intraspecific variation could mean that only a small proportion of animals within a population are responsible for most of the negative impacts – for instance when local human livelihoods [40,41] or conservation objectives [24,31,42] are threatened by individual predators with foraging specialisations. Individual variation can also lead to non-selective management strategies inadvertently selecting specific traits or demographic classes [2,43]. This has already been observed for species under selection from recreational hunting, where animals with 'bolder' personality types appear to be over-represented [35,44].

There is now considerable support for the notion that, in many situations where wildlife causes problems for people or conservation objectives, problem individuals are involved. This evidence can be direct, for example studies showing that specific individuals [36,45] and demographic classes [26] are disproportionately involved in incidents, or that problem behaviours are taught to offspring [33] or associates [34]. Indirect evidence points towards the involvement of problem individuals, where all animals contribute to an impact but to markedly varying degrees [46], or where sudden increases in impact are observed but are apparently unrelated to animal abundance [42].

(ii) Is It Possible to Accurately Identify and Target Problem Individuals?

Even if we know that subsets of animals are responsible for most of the problem, correctly identifying the problem individual(s) presents a key challenge in selective management [10]

Table 1. Examples of Methods for Targeting Animals and Their Assumed Accuracy in Selecting Specific Individuals.

Accuracy	Method	Example	Refs
Highest ↑	Targeting animals that can be individually recognised[a]	Using records of individual involvement to inform management	[22]
	Targeting individuals during human–wildlife impact event[a]	Enacting management actions during human–wildlife impact event	[34]
	Targeting individuals based on evidence from impact event[a,b]	Using tracking hounds to locate specific animals (also Box 2)	[87]
	Targeting individuals post impact event[b]	Targeting those individuals found at or near recent impact events	[50]
	Targeting individuals using specific lures, attractants, or traps[b]	Using specific lures or attractants aimed at those individuals most likely cause impact	[40]
	Targeting individuals within specific territories[b]	Removing animals when territory, not individual identity, is known	[24]
	Targeting individuals based on pre-established geographic areas[b]	Identifying specific areas where individuals are most likely to cause impact	[59]
	Targeting individuals based on problem animal profiling[c]	Identifying specific demographic classes within a population most likely to cause impact	[26]
	Population control or eradication[d]	Generalised control or eradication of a species	[10]
Lowest	Excluding access[d]	Attempting to exclude all individuals of a species from an area	[22]

[a]Selection Is Based on Identity.
[b]Selection Is Based on Location.
[c]Selection Is Based on Demographic Class.
[d]Method Is Assumed to Be Non-Selective.

Box 2. Methods for Exploring and Evaluating Problem Individual Management

To develop selective management, research that explores individuality and validates management strategies is needed and the toolbox for these tasks is expanding.

Exploring Individuality

Marking Animals. Marking with tags can facilitate individual identification, although this usually requires recaptures, resightings, or carcass recovery [21,44].

Camera Trapping and Image Analysis. This can help to identify the individuals involved in impacts when animals can be individually distinguished. Camera traps have been successfully used to identify problem individuals in terrestrial [88] and aquatic environments [40].

GPS and Other Tracking Technologies. These provide spatial data on individual movements that can be linked to human–wildlife impacts [46]. For example, by investigating the spatial clumping of puma *Puma concolor* locations, researchers found that only a minority of individuals were involved in livestock depredation [36].

Molecular Methods. These allow the forensic identification of individuals. For example, DNA fragments sampled from faeces [89] or attack wounds [90] have been used to identify individual animals responsible for crop and livestock losses.

Stable Isotope Analysis. A method that allows the relative contributions of different food items to the diet of an individual to be inferred [91]. This method has been used to help to identify food-conditioned bears [85] and crop-raiding elephants [92].

Evaluating Management

Removal Experiments. With random assignment to control and treatment groups, such experiments are considered to be the 'gold standard' for evaluating wildlife management [62]. Theoretical experiments that quantify the rate at which specific behaviours recur will help to inform the required frequency of management actions [32].

Analysis of Impact Records. This has allowed problem individual removal to be evaluated by observing the change in impact levels following treatments. Studies have focused on specific case studies [22] or have used data collected over broad areas for several years [11,58].

Analysis of Involvement Records. This requires data on individual animals. For example, by knowing which individual grizzly bears *Ursus arctos horribilis* were involved in impacts, Morehouse *et al.* [33] were able to link 'conflict behaviours' with social learning, and thereby critique guidelines for problem bear management.

Social Network Theory. This has the potential to advance our understanding of the social aspects of problem behaviour [32]. For example, Schakner *et al.* [34] used a network-based diffusion analysis to first demonstrate the social transmission of unwanted behaviours in California sealions *Zalophus californianus* and then to model the impact of management interventions.

(Figure 1). Three broad approaches emerge whereby animals can be targeted, based on individual identity, location, or demographic class (Table 1).

First, identifying those responsible can prove straightforward when individuals are marked (Box 2) or are easily distinguishable. The Kenyan Wildlife Service photographic database of African elephants *Loxodonta africana* involved in conflict incidents allows them to recognise repeat offenders [22]. This approach is also applicable where management action only requires the individual to be caught in the act of a single impact event. For example, in parts of South Africa any Cape fur seal *Arctocephalus pusillus* observed eating endangered seabirds can be shot [47].

Second, individuals can be targeted based on their location (Box 3). This approach should have highest accuracy if problems are spatially concentrated [48] and if management is conducted within a short timeof the impact [11] or during particular times when the impact is heaviest [41,49]. Again in Kenya, lions *Panthera leo* that have killed cattle have been targeted by traps

Box 3. Case Study – Managing Foraging Specialisations in Seals

In northern Scotland grey seals *Halichoerus grypus* (Figure I) and harbour seals *Phoca vitulina* are perceived to impact on fisheries through a reduction in Atlantic salmon *Salmo salar* available to recreational anglers [1]. Traditional management involved non-selective population reduction through culling seals at their haul-out sites [93], but was replaced with a more selective form of lethal removal following conservation and welfare concerns [94]. This new management regime attempted to remove individual seals by issuing licenses to trained marksmen to target individuals frequenting rivers and netting systems [49]. Graham *et al.* [41] set out retrospectively to test the efficiency of this strategy using photography to identify individual seals that were using rivers to forage. Their study provided evidence that only a small proportion (<1%) of the local seal populations were consistently sighted in rivers. They complemented this analysis with forensic methods suggesting that these 'river-specialist seals' had a higher proportion of salmonids in their diet than did seals found at haul-out sites [41]. Although this research falls short of quantifying the losses seals cause to recreational fisheries, it strongly suggests that river-specialist seals will have the greatest *per capita* impact. Indeed, despite requiring ongoing lethal control, the refinement of seal culling to these individuals represents a workable compromise for parties interested in both the protection of salmon stocks and the conservation of seals [94].

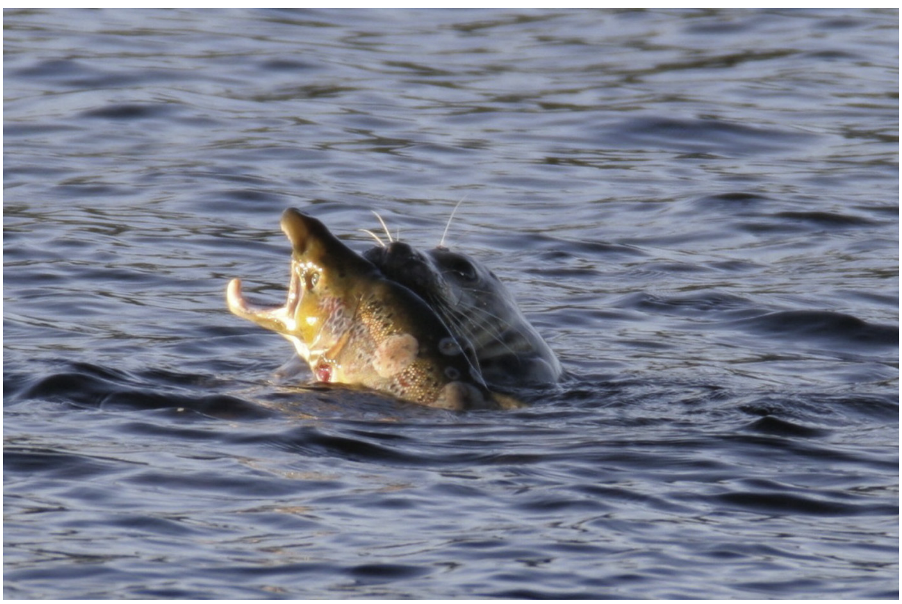

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Figure I. A Grey Seal *Halichoerus grypus* Eating a Mature Salmon on the River Ness, Scotland (Photo: ©Rob Harris, University of St. Andrews).

set near recent livestock kills [50]. However, zoning specific areas for removal should be considered with care. Ongoing removal coupled with rapid immigration of new problem animals or non-target animals might create a sink, or ecological trap, influencing the population dynamics of a much larger area [14,50,51]. To minimise this threat it has been suggested that problem individuals can be more effectively targeted if specific attractants [31] or trap designs [40] are used.

Third, several recent studies on managing wildlife have suggested that animals should be removed based on their demographic class [9,26,40,52,53]. In Australia, removing large male cats *Felis catus* is considered a conservation priority owing to their ability to take large native prey [26] while, in the Baltic Sea, adult male grey seals *Halichoerus grypus* are significantly more likely to be responsible for damage to fishing gear [52]. This classification has been described as 'predator profiling' [26], and we suggest the term **problem animal profiling** to allow its wider use in wildlife management.

Box 4. Case Study – 'Bruno the Bear' and the Power of the Individual

A single animal can sometimes have broad-reaching impacts, extending beyond ecology to international policy. Perhaps the most famous problem individual in recent decades was Bear JJ1 (Figure I). Named 'Bruno' by the media, in May 2006 this brown bear was the first to be recorded in Germany in 170 years [95]. While there was initially considerable positive attention at Bruno's arrival, a trail of well-publicised incidents, primarily the killing of livestock, led to Bruno being branded a 'problem bear' [95,96]. It is likely that Bruno's 'bad habits' were, at least in part, a product of his upbringing [33]; his mother had displayed similar behaviour during his infancy and his brother also went on to become a 'problem bear' [96,97]. While Bruno's individuality was perceived as errant by those who had been directly affected [96], it was seen as charismatic by others [95]. Although Bruno seemed to become less and less fearful of humans, his extensive roaming meant that attempts to capture him were unsuccessful, and he was eventually shot by hunters commissioned by the Bavarian government [96]. The decision to shoot Bruno was made following a rigorous risk assessment centred less on threats to livestock but more on evidence that he had become habituated to people and therefore posed an imminent threat to human safety [96]. By the time he was shot, the character of 'Bruno the Bear' had achieved international celebrity-like status. His death was reported in newspapers from *Das Spiegel* to *The Washington Post* with headlines such as 'Fed up Germany kills its only wild bear' (*Washington Post*, 27 June 2006). This single episode had policy implications at national and international levels. Within Germany, comparisons of public attitudes before and after Bruno suggested a significant decline in support for predator reintroductions, particularly in Bavaria [98]. At an international level, it prompted a special European Commission report focused on 'defining, preventing and reacting to problem bear behaviour' [97]. The story of Bear JJ1 vividly illustrates the impact of animal individuality.

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Figure I. A Taxidermy Mount of Bruno the Bear Raiding a Beehive, on Display at the Museum of Man and Nature, Munich, Germany (Photo: ©Museum Mensch und Natur).

With the exception of incidents where individuals can be recognised 'at the scene of the crime', we can otherwise assume that few strategies are perfectly accurate in their targeting (Table 1). Measures of targeting accuracy, sensitivity, or specificity (e.g. the proportion of true problem individuals identified and removed, the proportion of true 'innocent' individuals identified and removed) are therefore necessary to allow practitioners to evaluate alternative methods. While these evaluations can be supported by ecological data, forensic methods including detailed necropsies, stable isotope analysis, and DNA analysis might also prove useful (Box 2).

(iii) Does Targeting Problem Individuals Mitigate Impacts?

If problem individuals have been identified and a means of targeting them has been found, it is important to consider whether their removal will decrease impact and, if so, the timescale of any benefit (Figure 1). Wildlife managers can see the removal of individual animals as the only practical, humane, and cost-effective option available [16,24,34,54], even for species of conservation concern (Boxes 3 and 4). Indeed, if an uncommon behaviour, such as a foraging specialisation, is the cause of a problem, generalised measures to reduce impacts will likely fail if particular individuals are missed [26,30]. Where removal of the problem individual has been achieved, studies have reported minimal loss to the overall population [41,55], little stress to the remaining individuals [56], and both perceived [40] and actual [24,47,54] decreases in wildlife impact. On Stratton Island, USA, culling a single black-crowned night-heron *Nycticorax nycticorax* with a specialisation for eating common tern *Sterna hirundo* chicks resulted in the number of tern chicks per pair increasing from 0.42 to 1.9 [54]. In Namibia, after the translocation of 'problem leopards' *Panthera pardus*, livestock losses stopped for at least 16 months, despite new leopards moving into the vacated territory after only 6 weeks [57]. There are also circumstances where the timely removal of problem animals might minimise future interventions by preventing the spread of undesirable behaviours [34].

Despite these successes, many studies report that the benefits of removing problem individuals are short-lived [11,50,51]. The rapid recurrence of [51], or increase in [58], wildlife impact following the removal of individuals could indicate the presence of a **problem component** within the population [59], the social transmission of behaviours [34], compensatory immigration or population growth [17], a specific **site effect** [60], inadequate prevention measures [10], or behavioural changes in the residual population [61]. Whatever the cause, if benefits are short-lived and frequent interventions are necessary, increased ecological, economic, and social costs can be expected.

The utility of problem individual removal has been analysed in two cases using long-term datasets. Bradley *et al.* [11] compared the consequences for livestock losses of selectively and entirely removing packs of grey wolves *Canis lupus*. Although this study failed to identify those animals specifically responsible for predation, their analysis suggests that removing the breeding female, or a >1 year old male (the demographic class most likely to lead livestock hunts), did not significantly increase the time to reoccurrence of depredation compared to the effect of removing any other member of the pack. Furthermore, this study found that removing whole wolf packs reduced subsequent livestock depredation events by 79% over the next 5 years compared to 29% for partial pack removal [11]. At least in this situation, the selective removal of individual wolves was ineffective. Second, Artelle *et al.* [58] analysed attacks on humans and the consequent lethal control of grizzly bears *Ursus arctos horribilis* in Canada. They found evidence that the primary driver of these attacks was not the number of conflict-prone (risk-tolerant, bold) individual bears but shortages in their food supply [58]. This finding suggests that proactively addressing ecological stressors might be a better long-term strategy than reactive bear removal.

(iv) Can the Indirect Effects of Selective Management Be Avoided or Minimised?

Although there are promising non-lethal methods to mitigate wildlife impact (Box 1; see also [62,63]), problem individual management often involves the lethal removal of animals (Box 3). This removal is non-random, targeted at behaviours that create impacts, and is therefore likely to remove correlated phenotypes and demographic classes. While our focus is on removal of individuals for wildlife management purposes, our findings draw from, and are relevant to, animal populations under non-random selection from harvesting [43]. Following Greggor *et al.* [2], we consider the possible additional and unintended effects of selectivity (Figure 1). In selective management there is a general trend for males to be over-represented in removal records. This bias was first identified in relation to large carnivores [19], but is apparent in other taxa [3,51,64] and can be extremely pronounced. Only two of 38 seals caught raiding salmon traps in the Baltic Sea were female [40]. Only male Australian magpies *Cracticus tibicen* were observed attacking people [65]. In Kenya, male elephants were responsible for 86% of fence-breaking incidents [22]. In an attempt to refine lethal management, several recent studies have explicitly directed wildlife managers towards removing male animals [40,52,53]. The deliberate or unintentional targeting of males can, however, have detrimental effects; male removal and the skewing of natural sex ratios can alter community structure and sexual selection processes, produce an increase in infanticide and female harassment, and potentially remove the benefits of biparental care [66,67].

To reduce impacts in social species, individuals can be targeted to elicit behavioural change in others. This could be by removing individuals responsible for leading group behaviour. For example, the culling of specific alpha coyotes *Canis latrans* has been recommended to reduce livestock depredation by preventing cooperative killing behaviour [68]. Individuals might also be removed to induce a behavioural change in those animals that remain. Cromsigt *et al.* [9] have proposed utilising fear to induce behavioural change, stating 'it might be easier to induce fear for social ungulates where one individual is shot and escaping individuals learn about risk'. Aside from the unintended behavioural consequences of elevating the perception of risk [61], targeting individuals in group-living species carries additional uncertainty because of the uneven roles that individuals play in group dynamics. For instance, the removal of **keystone individuals** during management might have unforeseen negative consequences on the fitness of other individuals in the group through loss of knowledge or the destabilisation of social structures [32,67]. Modlmeier *et al.* [32] identify social network theory as a promising approach for investigating these concerns (Box 2).

In the longer term, selective management can exert a strong artificial selection against particular behaviours [50,69], possibly causing rapid changes to correlated phenotypes and genotypes [70]. Longstanding historical control of European brown bears *U. a. arctos* might have resulted in the selection of specific traits leading these bears to being better suited to coexistence with people than their North American counterparts [71]. Although it would appear that changing the behaviour of a population through the selective removal of individuals would be a win–win situation, the 'semi-domestication' of a species through trait selection can itself yield undesirable evolutionary effects by removing specific phenotypes [43,69].

(v) Can Targeting Individuals Help to Achieve Social Objectives?

Conservation conflicts can arise as a result of disagreement between parties over the methods or objectives of wildlife management [1]. Mitigating or working within these conflicts is often a difficult task because social variables, such as politics or stakeholder attitudes, can be of equal or greater importance to ecological variables in determining policy, practice, and outcomes [16,72]. While selective management itself is not typically seen as socially contentious, methods utilised to remove individuals, such as lethal control, can be (e.g., Box 4). An assessment is therefore needed as to whether focussing management on individual animals can help to navigate the diverse, and often opposing, attitudes, objectives, and ethical positions of a broad range of people (Figure 1).

The lethal control of wild animals is unpopular among those who value wildlife in an intrinsic and non-consumptive way [13]. However, it has been suggested that, compared to population control, removing only the problem individuals will create less of an impact upon the sensibilities of such groups [73]. This might be due to selective management being seen as 'more ethical' [34] or because the label of 'problem' or 'rogue' gives the animal a 'malicious agency' [23]. There certainly appears to be increased support for killing an individual once it has committed an act that could impact upon humans [74,75]. Despite these findings, lethal control is likely to be met with at least some opposition (Box 4).

Stakeholders who are negatively and directly impacted by wildlife rarely share the protectionist values of others [10], favouring hunting, population control [76], and translocation [3]. The perception that the impact is caused by an individual animal appears to catalyse calls for lethal control [23,25,27]. In Kenya, Maasai communities refused monetary compensation aimed at preventing retaliatory lion hunts because they perceived that individual lions had developed foraging specialisations on livestock that would continue indefinitely until those particular lions were removed [27]. Where appropriate, allowing stakeholders to participate actively in the hunting of problem animals might offer a form of bottom-up collaborative governance that promotes coexistence [8], especially if methods with high accuracy are used (Table 1).

Wildlife managers that choose to apply lethal control of individuals to ease social tensions tend to follow a utilitarian approach [77] wherein the removal of a few animals is acceptable compared to the negative consequences that other strategies (including inaction) might produce, such as a breakdown in trust between stakeholders and management agencies, or increased illegal persecution [4,27]. However, those that see problem individual management as a 'quick-fix method' with a 'high public relations value' [59] should be alert to the importance of correctly distinguishing between an improvement in stakeholder attitudes towards a management body and an improvement in attitudes towards the species [14]. Indeed, the assumption that the removal of a few individuals will increase tolerance of those remaining is often made by management bodies without clear evidence to suggest that this is the case [14]. Recent longitudinal studies attempting to unravel whether lethal grey wolf management increased stakeholder tolerance of wolves in the USA have found limited support for this assertion when surveying attitudes [75,76]. This assumption is fundamental to strategies that aim to promote coexistence and reduce illegal killing through control of problem individuals. Further studies across other systems are urgently needed to help those considering the social implications of selective management.

Concluding Remarks

We have looked at the ecological basis for, and efficacy of, selective wildlife management. As ethical and environmental concerns over traditional forms of wildlife management increase, it seems likely that the current trend toward selectivity will continue. Evidence is broadly supportive, and we are hopeful about what can be achieved and about prospects for future research (see Outstanding questions). Problem individuals can indeed be found in wild animal populations, and the clearest examples are found in generalist species with high behavioural plasticity. Tailoring management to focus on individual animals displaying unwanted traits, although at times logistically challenging, can generally be thought of as a less harmful strategy than population-level intervention. There are instances of where this selective management has produced sudden drops in impact, without threatening conservation objectives, and/or has presented a workable compromise for stakeholders with opposing views.

However, targeting problem individuals should not be seen as a general solution. The behaviour these animals display, although often uncommon, rarely appears to be truly exceptional. As a result, benefits can be short-lived as problem animals are replaced, meaning such strategies must rely on ongoing management, which is usually lethal. Where this is the case, in addition to increased economic costs, it seems likely that selection on particular traits, behaviours, or demographic classes will be strong and disruption to social dynamics is likely. Those responsible need to ensure that they have considered subtle and indirect impacts of these new selective processes.

For practitioners, decisions about selective management should be based on a combination of the economic, ecological, and social costs and benefits (Figure 1). A decision-making process that is both transparent and flexible should help to account for any uncertainty or change in

Outstanding Questions

We highlight four areas of research that will add to our understanding of the ecology of problem individual management.

(i) What are the ecological drivers of problem behaviours, and can proactive management of such drivers alleviate impact and conflict?

(ii) Can we build end-to-end ecological appraisals of selective management, where the behaviour and biology of individuals are used to understand problems, develop solutions, and evaluate actions in practice?

(iii) In which environmental contexts is management confounded by rapid re-emergence of problem behaviours?

(iv) Can we effectively integrate ecology and social science in developing mitigation options and investigating the longer-term effects of selective management on those affected by, and engaging with, the problem?

these variables [1,78]. Ultimately, management will benefit greatly from improved understanding of the underlying causes of problem behaviours (e.g., [33,34,58]). Such research, though rare, represents the best long-term prospect for mitigating, minimising, and preventing impact and conflict.

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