



Review

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Parasite insight: assessing fitness costs, infection risks and foraging benefits relating to gastrointestinal nematodes in wild mammalian herbivores

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Mammalian herbivores are typically infected by parasitic nematodes, which are acquired through direct, faecal–oral transmission. These parasites can cause significant production losses in domestic livestock, but much less is known about impacts on wild mammalian hosts. We review three elements of parasitism from the host's perspective: fitness costs of infection, risks of infection during foraging and benefits of nutritious pasture. The majority of wildlife studies have been observational, but experimental manipulation is increasing. Treatment with anthelmintics to manipulate parasite load has revealed varied impacts of parasites on fitness variables across host species, but has not produced consistent evidence for parasite-induced anorexia or impaired body condition. Some experimental studies of infection risk have manipulated faecal contamination and detected faecal avoidance by hosts. Only two field studies have explored the trade-off between infection risk and nutritional benefit generated by avoidance of contaminated patches. Overall, field studies of costs, risks and benefits of the host–parasite relationship are limited and few have examined more than one of these elements. Parasitism has much in common with predation, and future insights into anti-parasite responses by wild hosts could be gained from the conceptual and technical developments in research on anti-predator behaviour.

This article is part of the Theo Murphy meeting issue 'Evolution of pathogen and parasite avoidance behaviours'.

1. Background

Mammalian herbivores are typically infected by a suite of gastrointestinal helminth parasites, primarily nematodes (figure 1). In domestic livestock, gastrointestinal parasites cause losses to agricultural production throughout the world [1]. The impacts of parasitism on livestock can be severe, arising from pathological changes to the gastrointestinal tract [2,3]. However, many impacts are sub-clinical, acting through suppression of appetite and impaired assimilation of forage: loss of body condition [4], lower growth rate [5] and reduced reproductive output [6]. To minimize production losses, anthelmintic compounds have been used routinely to treat livestock, particularly sheep, *Ovis aries*, and goats, *Capra hircus*, for decades [7].

In contrast to domestic livestock, much less is known about the interactions between gastrointestinal parasites and the wild mammalian hosts they have co-evolved with. Early studies of mass mortality of eastern grey kangaroos (*Macropus giganteus*) [8] and Soay sheep (a wild, insular form of domestic sheep) [9] found



Figure 1. Nematode parasites in the stomach of a healthy adult male eastern grey kangaroo (*Macropus giganteus*). The larger parasites (*Labiosimplex* spp.) are about 100 mm in length and occur in numbers up to 500. The smaller parasites, predominantly *Pharyngostromylus kappa*, *Rugopharynx* spp. and *Cloacina* spp., typically occur in tens of thousands. Photo by Graeme Coulson. (Online version in colour.)

heavy nematode burdens, extensive gastrointestinal lesions and marked haematological and biochemical changes. Gulland [9] suggested that immunosuppression interacting with poor forage conditions led to the mortalities in Soay sheep. However, mortality events such as these are exceptional. Recent studies have reported more subtle, sub-clinical symptoms similar to those seen in domestic stock, particularly poorer body condition [10,11] and lower fecundity [12,13]. Nevertheless, establishing the casual relationships involved in fitness changes is challenging when working with free-ranging mammalian herbivores. Unbiased sampling, experimental manipulation and extended monitoring pose far greater logistical challenges in wildlife than for livestock [14], so field experiments are rare. Consequently, our current understanding of the true costs of parasitism in wild herbivores is limited [15].

The challenges of working with wildlife also apply to other elements of the host–parasite relationship. A common behavioural strategy adopted by a host to reduce the risk of infection is simply to avoid sources of parasites [16,17]. Domestic sheep [18], cattle, *Bos taurus* [19] and horses, *Equus caballus* [20], have all been shown to avoid faeces while foraging, thereby reducing their risk of ingesting infective larvae on the surrounding pasture. Paradoxically, this avoidance behaviour creates patches of pasture that are taller, due to reduced offtake, and more nutritious, due to the fertilizing action of faeces [21]. Foraging hosts then face a trade-off between the risks of acquiring parasites and the benefits of foraging in the most nutritious patches [21] (figure 2). Trade-offs between parasite risk and foraging benefit are well documented in domestic livestock [22,23], but the few studies of free-ranging hosts are equivocal [24].

The aim of this review is to evaluate the evidence for three major elements of the relationship between parasitic gastrointestinal nematodes and their wild mammalian herbivore hosts. We review: (i) the fitness costs of infection incurred by the host, (ii) the risk of infection as the host forages, and (iii) the benefits (potentially foregone) of foraging in patches of high-quality pasture. We specifically distinguish between evidence that is essentially observational, also referred to as correlational or cross-sectional, versus findings from experimental manipulation, which we favour because only an experiment can

elucidate the direct effects of a variable [25]. We also distinguish between studies of wildlife held in captivity versus field studies of free-ranging host species, to which we give more weight.

2. Fitness costs

Studies of host–parasite relationships in mammalian herbivores cover a range of host taxa (table 1). Details of parasite identification vary between studies, but all involve nematodes from the order Strongylida and from the two superfamilies Strongyloidea and Trichostrongyloidea (table 1). In some studies, identification beyond this level has not been undertaken; in others, we have extrapolated from other studies to list the nematode taxa presumed to be present. In studies based on faecal examination, eggs could not be identified further than the ordinal level, so are referred to as ‘strongylids’.

The use of faecal egg counts to assess parasite burdens has potential pitfalls. This method has been used extensively in small ruminants, where egg counts can be affected by faecal consistency, host immunity and differing fecundity of the nematode species present [52]. Host size also influences the utility of faecal egg counts, making them of very limited value in cattle [52]. In wild animals, the relationship between faecal egg counts and parasite burdens needs to be evaluated beforehand [52], which has been done in very few studies. In one case, Seiwright *et al.* [53] obtained a high correlation (+0.88) between egg counts and parasite burden of *Trichostrongylus tenuis* in red grouse, *Lagopus lagopus scoticus*, while in another, Cripps *et al.* [54] found a much lower overall correlation (+0.40) between egg counts and total burdens of cloacinine nematodes in eastern grey kangaroos, with the contribution varying between nematode genera. Many other studies rely on faecal egg counts (table 1), but with the exception of Morgan *et al.* [43], have not established a relationship with parasite burdens.

The majority of studies of fitness costs have taken an observational approach. Some have explored relationships between parasite load and demography of the host population. In saiga antelope (*Saiga tatarica*), for example, Morgan *et al.* [43] found that one nematode species (*Nematodirus gazellae*) occurred at



Figure 2. Free-ranging mammalian herbivores foraging on pasture heavily contaminated with conspecific faeces. (a) Adult female eastern grey kangaroo (*Macropus giganteus*) at Anglesea, Victoria, Australia. (b) Adult female Soay sheep (*Ovis aries*) at Hirta, St Kilda, Scotland, UK. Photos by Graeme Coulson. (Online version in colour.)

highest intensities (i.e. mean number of parasites per infected host) in antelope of about 2–3 years old, while the intensity of others (*Marshallagia* spp.) increased with age, albeit at a declining rate. Other studies have compared populations or classes (i.e. sex, age, reproductive status) within populations expected *a priori* to differ in their vulnerability to parasite infection or in the impact of parasitism on their fitness. For example, Arundel *et al.* [28] contrasted the parasites of free-ranging red kangaroos (*Osphranter rufus*) with those at a higher density in an enclosed reserve, but found no difference in nematode species composition, prevalence or abundance.

The fundamental limitation of all such observational studies is that they cannot resolve the causal relationships involved: an association between host and parasite variables does not necessarily imply causation, much less determine the direction of any causal link [55]. Observed correlations are also potentially confounded by intrinsic differences among individual hosts (e.g. [56]). Nonetheless, dubious interpretations pervade the literature. In a study of plains zebra (*Equus quagga*), for example, Fugazzola & Stancampiano [35] found that dominance rank covaried with total parasite eggs shed in faeces: dominant stallions shed fewer eggs. While acknowledging that the direction of causality was ‘controversial’, the authors

nonetheless concluded that dominance rank ‘does influence’ egg shedding, arguing that dominance engenders better body condition in plains zebras, which in turn may confer increased resistance and immunity to infection. However, the authors did not consider the alternative argument that inherently better body condition in some stallions boosted both their competitive ability and immune response, and their correlational study was unable to distinguish between these or other plausible explanations.

Many of the limitations of observational studies can be overcome by experimental manipulation, and an encouraging number of studies of fitness costs have taken this approach (table 1). Commercial anthelmintics offer a powerful tool to manipulate the host’s parasite load [14,57]. As a first step, it is essential to confirm the efficacy of the anthelmintic treatment in wild hosts, and ensure that there are no unwanted side-effects [14,58]. Off-label anthelmintic treatment of wildlife hosts can have unexpected effects. For example, treating Svalbard reindeer (*Rangifer tarandus platyrhynchus*) with moxidectin depressed the abundance of *Ostertagia gruehneri* for six months, but had no effect on the other dominant species, *Marshallagia marshalli* [12]. Similarly, treating eastern grey kangaroos with two macrocyclic lactones (ivermectin and

Table 1. Details of studies of fitness costs, infection risk and foraging benefit in wild mammalian herbivore hosts and their principal nematode parasites. The principal parasites involved (or presumed to be involved) in studies are listed to Order and Family level where possible, or otherwise to Order and Superfamily, based on the classification of Gibbons [26]. Observational (Obs.) and manipulative (Man.) study components are listed under cost, risk and benefit elements. Codes for study descriptors are given in the footnotes to the table. *Study descriptors.* Level of host resolution: I, individual animal (tagged or identified in some way); P, populations or population class (age/sex/status). Host behavioural response: G, grazing behaviour (including diet); L, latrine use. Host fitness measures: B, body condition (including growth); H, haematological values; R, reproductive status; X, mortality. Intrinsic host covariates: D, dominance rank; M, morphological trait. Extrinsic environmental covariates: S, season; V, vegetation types; W, water (soil moisture or rainfall). Experimental manipulation: A, anthelmintic treatment; F, food supplementation; C, contamination with faeces.

mammalian herbivore host	principal nematode parasites	source	cost		risk		benefit	
			Obs.	Man.	Obs.	Man.	Obs.	Man.
Marsupialia								
Phalangeridae								
mountain brushtail possum (<i>Trichosurus caninus</i>)	Strongylida: Trichostrongylidae	Viggers <i>et al.</i> [27] ^d		A H I R				
Macropodidae								
red kangaroo (<i>Osphranter rufus</i>)	Strongylida: Cloacimidae	Arundel <i>et al.</i> [28]	P S					
eastern grey kangaroo (<i>Macropus giganteus</i>)	Strongylida: Cloacimidae	Arundel <i>et al.</i> [8]	H P S					
		Garnick <i>et al.</i> [24]			G	C G	C G	F G
		Cripps <i>et al.</i> [29] ^d		A B H I				
		Cripps <i>et al.</i> [30] ^d					A G I	
		V. Bristow, G. Coulson & I. Beveridge 2003 (unpublished data; electronic supplementary material)					C G P	
red-necked wallaby (<i>Notamacropus rufogriseus</i>)	Strongylida: Cloacimidae	Sharp <i>et al.</i> [31]					C G I	
Lagomorpha								
Leporidae								
mountain hare (<i>Lepus timidus</i>)	Strongylida: Trichostrongylidae	Newey & Thirgood [13]		A B I R X				
snowshoe hare (<i>Lepus americanus</i>)	Strongylida: Trichostrongylidae	Murray <i>et al.</i> [32,33]		A F I X				
Rodentia								
Sciuridae								
red squirrel (<i>Tamiasciurus hudsonicus</i>)	Strongylida: Strongyloidea	Gooderham & Schulte-Hostedde [34] ^d	P R					
Perissodactyla								
Equidae								
plains zebra (<i>Equus quagga</i>)	Strongylida: Strongyloidea	Fugazzola & Stancampiano [35] ^d	D P					
		Turner & Getz [11] ^d	P S					
Artiodactyla								
Cervidae								

(Continued.)

Table 1. (Continued.)

mammalian herbivore host	principal nematode parasites	source	cost		risk		benefit	
			Obs.	Man.	Obs.	Man.	Obs.	Man.
caribou (<i>Rangifer tarandus</i>)	Strongylida: Trichostrongylidae	Hughes <i>et al.</i> [10]	CP					
Svalbard reindeer (<i>Rangifer tarandus platyrhynchus</i>)	Strongylida: Trichostrongylidae	Arneberg <i>et al.</i> [36] ^{b,d}		ACGI				
		Arneberg & Folstad [37] ^{b,d}		ACGI				
		van der Wal <i>et al.</i> [38] ^d	IGW				CG	
		Stien <i>et al.</i> [12]	BPR				IACR	
red deer (<i>Cervus elaphus</i>)	Strongylida: Trichostrongylidae	Irvine <i>et al.</i> [39] ^d	PBR					
Bovidae								
blue wildebeest (<i>Connochaetes taurinus</i>)	Strongylida: Trichostrongylidae	Turner & Getz [11] ^d	PS					
springbok (<i>Antidorcas marsupialis</i>)	Strongylida: Trichostrongylidae	Turner & Getz [11] ^d	PS					
		Turner <i>et al.</i> [40] ^d	CPSW					
dik-dik (<i>Madoqua kirkii</i>)	Strongylida: Strongyloidea ^a	Ezenwa [41]				L	FG	
Grant's gazelle (<i>Nanger granti</i>)	Strongylida: Strongyloidea ^a	Ezenwa [41]				L		
	Strongylida: Strongyloidea ^a	Worsley-Tonks & Ezenwa [42] ^{b,d}					AIG	
saiga antelope (<i>Saiga tatarica</i>)	Strongylida: Trichostrongyloidea	Morgan <i>et al.</i> [43] ^d	BP					
African buffalo (<i>Syncerus caffer</i>)	Strongylida: Trichostrongylidae	Ezenwa & Jolles [44] ^d	BHMP					
		Budischak <i>et al.</i> [45] ^d	BCHP					
bushbuck (<i>Tragelaphus scriptus</i>)	Strongylida: Strongyloidea ^a	Apio <i>et al.</i> [46]				GIL		
Alpine ibex (<i>Capra ibex</i>)	Strongylida: Trichostrongylidae	Brambilla <i>et al.</i> [47]				GP		
Soay sheep (<i>Ovis aries</i>)	Strongylida: Trichostrongylidae	Gulland [9] ^c	BH	APX				
		Hutchings <i>et al.</i> [48] ^b					ACG	AFG
		Jones <i>et al.</i> [49]					AGI	
		Craig <i>et al.</i> [50] ^d	PB					
chamois (<i>Rupicapra rupicapra</i>)	Strongylida: Trichostrongylidae ^a	Fankhauser <i>et al.</i> [51] ^c						CG
gemsbok (<i>Oryx gazelle</i>)	Strongylida: Trichostrongylidae	Turner & Getz [11] ^d	CPSW					
impala (<i>Aepyceros melampus</i>)	Strongylida: Strongyloidea ^a	Ezenwa [41] ^d				L		

^aParasites not specified.

^bCaptive study.

^cPartly captive study.

^dFaecal egg counts.

moxidectin) showed that both had poor efficacy in controlling strongylid nematodes [58]. Of even greater concern, treating red-legged pademelons (*Thylogale stigmatica*) with a benzimidazole (mebendazole) caused 80% mortality in the hosts [59]. Ten experimental studies of fitness costs have used anthelmintics (table 1) and all prudently tested for efficacy. Together these studies have developed our understanding of the variation and complexity of impacts of parasites on a range of fitness variables across host species. For example, anthelmintic treatment of Svalbard reindeer reduced the abundance of one of two major parasite species, and both body condition and fecundity increased in treated hosts [12]. By contrast, treating mountain hares (*Lepus timidus*) with an anthelmintic reduced abundance of the parasite *Trichostrongylus retortaeformis* and increased fecundity of the hosts, relative to a control group, but did not change host body condition or over-winter survival [13].

Anthelmintic treatments have also been used to investigate suppression of appetite in free-ranging hosts. Parasite-induced anorexia is commonly observed in domestic livestock and can result in serious production losses [60]. The adaptive significance of this paradoxical response is debated, but most likely acts to promote an immune response by the host, and may also allow the host to forage more selectively to seek less contaminated pasture or plant species with anti-parasite properties [61,62]. In wildlife studies, however, the evidence for parasite-induced anorexia is ambiguous. Arneberg *et al.* [36] treated captive, semi-domesticated reindeer (*Rangifer tarandus tarandus*) calves with an anthelmintic: daily food intake of the treatment group increased over time compared with placebo-treated controls, consistent with anorexia. Similarly, Worsley-Tonks & Ezenwa [42] treated free-ranging female Grant's gazelles (*Nanger granti*) with an anthelmintic and reported a higher allocation of time to foraging compared with untreated controls. In contrast, Jones *et al.* [49] could not detect any effect of anthelmintic treatment on food intake or diet selection in either sex of free-ranging Soay sheep, nor could Cripps *et al.* [30] detect any effect of treatment on four foraging variables in a before-after-control-impact experiment on free-ranging adult female eastern grey kangaroos.

In a more elaborate experiment, Murray *et al.* [32] manipulated both parasite burden and nutritional stress in the snowshoe hare (*Lepus americanus*) by treating hares with an anthelmintic and providing supplementary food; predation was the overwhelming cause of mortality, and survival was influenced synergistically by parasites and nutrition when food availability was limited. These findings conform to Beldomenico & Begon's [63] 'vicious circle' of synergistic effects between body condition and parasite infection in wildlife. The authors argued that wild hosts would have greater inherent variation in susceptibility to parasites than would their domestic counterparts. Wild hosts are then subject to a positive feedback loop between body condition and parasite infection: poor condition predisposes individuals to infection, which then reduces the condition of the host, further predisposing the host to infection. If valid, this feedback model could help to resolve some of the uncertainty about the causal relationship between body condition and infection variables.

In summary, our understanding of the fitness costs imposed by gastrointestinal parasites on their free-ranging herbivores has advanced greatly since the early studies of Soay sheep and kangaroos (table 1). Observational studies made initial contributions, but have been largely superseded by more powerful, field-based, manipulative experiments.

However, studies have been heavily reliant on faecal egg counts, which are often an inadequate or unproven measure of parasite burden. So far, no clear signal has emerged for the effect of parasite infection on body condition or spontaneous anorexia.

3. Infection risks

Strongyloid gastrointestinal nematodes are acquired by their mammalian hosts through direct, faecal–oral transmission: eggs are shed onto the sward and develop to the infective L3 stage, which can then be ingested by hosts as they forage [64]. Hosts are unable to detect larvae, but the presence of faecal material provides a visual and olfactory cue to likely larval concentrations on the sward [23]. Hart [16,17] pointed out that hosts could reduce their exposure to infective larvae in two ways: by avoiding faecal contamination while foraging and by defaecating at discrete latrine sites, which are then avoided during foraging.

Nine of the studies of infection risk in free-ranging mammalian herbivores have taken an observational approach (table 1). Two of these assessed the density of parasite larvae in different habitats. Vegetation types with the highest natural concentrations of larvae were avoided when grazing by both Svalbard reindeer [38] and Soay sheep [48]. Two others compared faecal contamination in areas grazed and avoided along the foraging paths of hosts. Eastern grey kangaroos took fewer bites per step along paths with greater faecal contamination [24] and, similarly, Alpine ibex (*Capra ibex*) grazed preferentially in patches with lower faecal contamination [47]. Two more studies examined larval density near latrines. Ezenwa [41] found that strongyle larval density in the vicinity of latrines of three antelope host species was higher than in control areas, as would be expected. By contrast, Apio *et al.* [46] detected no difference between bushbuck (*Tragelaphus scriptus*) latrines and control areas in terms of larval density, and found that foraging rates of bushbuck were higher within latrines. The interpretation of this unexpected finding was that the primary function of latrines in bushbuck may be olfactory communication among conspecifics.

Ezenwa [41] conducted the first manipulation of the perceived risk of infection by altering the level of faecal contamination encountered by hosts as they foraged. She provided free-ranging dik-dik (*Madoqua kirkii*) with supplementary food in paired piles, one with dried dik-dik faecal pellets adjacent to the food and one without faecal contamination. Dik-dik showed a strong preference to feed on uncontaminated rather than contaminated piles, taking more than four times as many bites at uncontaminated piles. However, Ezenwa also found that larval density was elevated in areas surrounding latrines, leading to an increased risk of parasitism when foraging, so an anti-parasite strategy may not be the primary function of latrines in this species. V. Bristow, G. Coulson & I. Beveridge 2003 (unpublished data; electronic supplementary material) also investigated faecal avoidance by manipulating the level of faecal contamination encountered by foraging hosts. Bristow *et al.* established a randomized chequerboard of contaminated and uncontaminated cells in a grassy clearing, then observed free-ranging eastern grey kangaroos foraging across the site. Overall, adult hosts showed no significant preference for either cell type. By contrast, 80% of sub-adults preferred uncontaminated cells, consistent with their greater vulnerability to

infection with *Globocephaloides trifidospicularis* (Trichostrongyloidea) [8]. There were also differences related to the costs of reproduction. Adult females with high lactational demands showed no preference, whereas 66% of adult females with negligible reproductive costs preferred uncontaminated cells, suggesting that heavily-lactating females foraged indiscriminately in order to maintain intake [65].

Two experiments have examined aversion to faeces of species other than those of the host. Fankhauser *et al.* [51] tested free-ranging chamois (*Rupicapra rupicapra*) for aversion to faeces of domestic sheep, which overlap widely with chamois in habitat and nematode parasite communities, including a prevalent and potentially pathogenic species *Teladorsagia circumcincta*. No change in grazing intensity on plots contaminated with sheep faeces following a pre-treatment 'control' phase, nor on untreated plots or plots containing inert 'dummy' faeces, was detected. However, Fankhauser *et al.* did not test for aversion to the faeces of conspecifics, so it was unclear whether chamois simply lacked a faecal avoidance response or did not respond to sheep faeces in the way they might have if exposed to chamois faeces. In a similar experiment, Sharp *et al.* [31] showed that red-necked wallabies (*Notamacropus rufogriseus*) were not deterred from supplementary food by faecal contamination *per se*. Wallabies were offered supplementary food contaminated with faeces of conspecifics or with faeces of sympatric eastern grey kangaroos and western grey kangaroos (*Macropus fuliginosus*), which share few parasite species with red-necked wallabies [66]. Wallabies showed strong discrimination, consuming five times more food contaminated with heterospecific faeces than with conspecific faeces.

In summary, observational and experimental studies of free-ranging herbivores provide consistent evidence of faecal avoidance as a strategy to reduce their exposure to infective larvae. The role of latrines in reducing larval exposure is less evident, and may be secondary to a social signalling function. Avoidance of faeces of other species has received little attention to date, but is amenable to field experimentation which suggests that herbivore responses can be quite subtle.

4. Foraging benefits

Herbivores must weigh up the parasite risk and the nutritional benefit of food as they forage [67]. In free-ranging mammalian herbivores, only two field studies have explored the nutritional benefits of foraging on pasture potentially contaminated with parasite larvae, and both have coupled the putative benefits with the ongoing risks of acquiring parasites (table 1). In a study of free-ranging Soay sheep, Hutchings *et al.* [48] measured the quantity and quality of pasture in two vegetation strata on the island of Hirta, St Kilda, together with the abundance of infective nematode larvae in these strata throughout the year. In spring, the greatest seasonal disparity in sward height between the two strata coincided with the highest abundance of larvae. Foraging observations showed that overall, sheep avoided this tall but risky sward particularly in spring, thus trading off a nutritional benefit in favour of minimizing their parasite risk.

Garnick *et al.* [24] have conducted the only experiment on the risk–benefit trade-off, simultaneously manipulating faecal contamination and sward height in a study of free-ranging eastern grey kangaroos at Serendip Sanctuary, southeastern Australia.

Garnick *et al.* installed small enclosures to allow pasture to grow taller than the surrounding matrix, removed faecal pellets from half of the plots and added pellets to other half, giving two levels of sward height and two levels of faecal contamination in a factorial design. Foraging observations showed that both sward height and faecal contamination affected the choice of foraging patches: kangaroos preferred taller grass overall, but would not trade-off the higher parasite risk of contaminated patches for an increase in nutrient intake.

Together these two studies illustrate some of the complex choices facing free-ranging herbivores when they forage. A grazing sward presents both temporal and spatial variation in forage quality and quantity, together with faecal contamination and its associated infection risk. The limited evidence indicates that herbivores prioritize faecal avoidance over forage intake, but the limits to this trade-off are yet to be explored in any depth.

5. Gaining insight

As hosts to parasitic nematodes, mammalian herbivores encounter potential fitness costs, infection risks and foraging benefits. Some progress has been made towards understanding these elements, initially from observational studies and more recently through the increased use of field experiments (table 1). However, experimental approaches have been rather tentative to date. Most field studies have manipulated only one of the three elements of cost, risk and benefit, although Garnick *et al.* [24] manipulated both risk and benefit variables. This contrasts strongly with studies of domestic livestock. Fleurance *et al.* [20], for example, simultaneously manipulated infection status, faecal contamination and sward height in their study of nutritional and anti-parasite strategies in foraging horses. Working with wildlife poses undeniable challenges for field experimentation [14], but much can be gained from theoretical and technical developments. In this section, we consider the prospects for manipulative studies of fitness costs, infection risks and foraging benefits in free-ranging hosts.

The standard approach to assessing fitness costs of parasitism involves treatment with anthelmintics, followed by a comparison of the performance of treated hosts with untreated controls. One limitation of this approach is that co-infections with multiple parasite species or strains are commonplace [68], yet anthelmintics are typically broad spectrum, affecting multiple nematode taxa [57]. As a result, the contribution of each taxon to any observed effect on fitness cannot be isolated [28]. Even if more targeted therapies became available, interpretation of species-specific impacts on hosts would be problematic due to complex competitive and facilitative interactions among parasite taxa [68]. Another clear limitation of anthelmintic treatment is that the duration of action is typically a small proportion of the lifespan of the host, yet hosts carry chronic infections because they are constantly reinfected as they forage. Assessing fitness costs at a lifetime scale would, therefore, be a more meaningful and likely more sensitive measure. While this would be more logistically demanding, fitness costs of parasites could be integrated into long-term, individual-based studies of free-ranging animals, which have proven their worth in ecology and evolutionary biology [69].

The infection risk posed by parasites and the foraging benefits to hosts involve questions about animal behaviour

[16,17], and the discipline of behavioural ecology has much to offer in both theoretical perspectives and practical techniques. Raffel *et al.* [70] argued that parasitism and predation are functionally equivalent in most respects, despite their fundamental differences, so theoretical and empirical developments can provide mutual insights. One example is the risk allocation hypothesis, which was developed for prey species foraging under the threat of predation [71,72], but has obvious application to host–parasite interactions as well. The risk allocation hypothesis recognizes that predation risk can vary temporally, with alternating states of high and low risk. One counterintuitive prediction is that prey exposed to chronic high risk are forced to reduce their time allocated to anti-predator behaviour in order to maintain their food intake [72], which has clear parallels to a herbivore foraging on a heavily contaminated yet nutritious grassy sward. The concept of a landscape of fear [73,74] is also applicable to parasite risk. This concept describes a three-dimensional virtual landscape, with peaks and valleys of probability reflecting the differing levels of predation risk across spatial variation in habitat type or structure. A landscape of fear could apply equally to parasite risk [75], particularly where infective larvae are aggregated, such as in moist habitat [38,48] and around latrines [41].

Rigorous behavioural assays devised for anti-predator responses can also be applied to anti-parasite behaviours. A prime example is ‘giving up density’ [76]. This is a measure of the density of food resources within a patch at which an individual ceases foraging, corresponding to a harvest rate that balances the metabolic costs and predation risks of foraging. Again, this measure can be readily adapted to assessing the parasite infection risk associated with foraging (e.g. [31]). In terms of technological developments, motion-sensitive camera traps can be used to monitor behaviour at focal sites such as latrines, experimental plots or supplementary food [77,78]. At a wider spatial scale, animal-borne video cameras [79,80] can be fitted to monitor hosts as they forage over a sward peppered with faeces. Incorporating conceptual and technical approaches such as these will sharpen the focus and boost the impetus of research into anti-parasite behaviour in free-ranging mammalian hosts.

References

- Coyne MJ, Smith G. 1994 Trichostrongylid parasites of domestic ruminants. In *Parasitic and infectious diseases: epidemiology and ecology* (eds ME Scott, G Smith), pp. 235–247. San Diego, CA: Academic Press.
- Fox M. 1997 Pathophysiology of infection with gastrointestinal nematodes in domestic ruminants: recent developments. *Vet. Parasitol.* **72**, 285–308. (doi:10.1016/S0304-4017(97)00102-7)
- Colditz IG. 2008 Six costs of immunity to gastrointestinal nematode infections. *Parasit. Immunol.* **30**, 63–70. (doi:10.1111/j.1365-3024.2007.00964.x)
- Loyacano A, Williams J, Gurie J, DeRosa A. 2002 Effect of gastrointestinal nematode and liver fluke infections on weight gain and reproductive performance of beef heifers. *Vet. Parasitol.* **107**, 227–234. (doi:10.1016/S0304-4017(02)00130-9)
- O’Kelly JC, Post TB, Bryan RP. 1988 The influence of parasitic infestations on metabolism, puberty and first mating performance of heifers grazing in a tropical area. *Anim. Reprod. Sci.* **16**, 177–189. (doi:10.1016/0378-4320(88)90011-5)
- Liu SM, Masters DG, Adams NR. 2003 Potential impact of nematode parasitism on nutrient partitioning for wool production, growth and reproduction in sheep. *Aust. J. Exp. Agr.* **43**, 1409–1417. (doi:10.1071/EA03017)
- Barragry T. 1984 Anthelmintics—a review. *N. Z. Vet. J.* **32**, 161–164. (doi:10.1080/00480169.1984.35109)
- Arundel JH, Dempster KJ, Harrigan KE, Black R. 1990 Epidemiological observations on the helminth parasites of *Macropus giganteus* Shaw in Victoria. *Wildl. Res.* **17**, 39–51. (doi:10.1071/WR9900039)
- Gulland FM. 1992 The role of nematode parasites in Soay sheep (*Ovis aries*) mortality during a population crash. *Parasitology* **105**, 493–503. (doi:10.1017/S0031182000074679)
- Hughes J, Albon SD, Irvine RJ, Woodin S. 2009 Is there a cost of parasites to caribou? *Parasitology* **136**, 253–265. (doi:10.1017/S0031182008005246)
- Turner WC, Getz WM. 2010 Seasonal and demographic factors influencing gastrointestinal parasitism in ungulates of Etosha National Park. *J. Wildl. Dis.* **46**, 1108–1119. (doi:10.7589/0090-3558-46.4.1108)
- Stien A, Irvine RJ, Ropstad E, Halvorsen O, Langvatn R, Albon SD. 2002 The impact of gastrointestinal

6. Conclusion

The fitness costs, infection risks and foraging benefits associated with gastrointestinal parasitism are relatively well understood in domestic mammalian herbivores. This is due, in part, to the relative ease of manipulating these systems experimentally. Our understanding of these costs, risks and benefits is much less clear for their wild counterparts, particularly as most studies of free-ranging mammalian herbivores have been observational. However, some elegant experiments have revealed consistent patterns in the wild: fitness costs of gastrointestinal parasitism are not strongly reflected in appetite suppression or body condition; faecal avoidance is a widespread strategy to minimize infection risk; faecal avoidance is generally prioritized over forage intake. Further experiments with wild mammalian herbivores should capitalize on novel technology and ecological theories initially developed for anti-predator behaviours. These approaches should help to elucidate the role of latrines in reducing larval exposure, the costs and benefits of interspecific faecal aversion, and the limits to the trade-off between faecal aversion and forage intake, among others.

Data accessibility. Data are available in the electronic supplementary material.

Authors’ contributions. G.C. conceived the review, coordinated the study and drafted the manuscript; J.K.C. sourced most publications, developed many of the ideas and helped draft the manuscript; S.G. developed more of the ideas and helped draft the manuscript; V.B. devised and conducted the checkerboard experiment and helped draft the manuscript; I.B. provided essential parasitological input and helped draft the manuscript. All authors gave final approval for publication.

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- nematodes on wild reindeer: experimental and cross-sectional studies. *J. Anim. Ecol.* **71**, 937–945. (doi:10.1046/j.1365-2656.2002.00659.x)
13. Newey S, Thirgood S. 2004 Parasite-mediated reduction in fecundity of mountain hares. *Proc. R. Soc. Lond. B* **271**, S413–S415. (doi:10.1098/rsbl.2004.0202)
 14. Irvine RJ. 2006 Parasites and the dynamics of wild mammal populations. *Anim. Sci.* **82**, 775–781. (doi:10.1017/ASC2006106)
 15. Gunn A, Irvine RJ. 2003 Subclinical parasitism and ruminant foraging strategies: a review. *Wildl. Soc. Bull.* **31**, 117–126.
 16. Hart BL. 1990 Behavioral adaptations to pathogens and parasites: five strategies. *Neurosci. Biobehav. Rev.* **14**, 273–294.
 17. Hart BL. 1992 Behavioral adaptations to parasites: an ethological approach. *J. Parasitol.* **78**, 256–265. (doi:10.2307/3283472)
 18. Hutchings MR, Kyriazakis I, Anderson DH, Gordon IJ, Coop RL. 1998 Behavioural strategies used by parasitized and non-parasitized sheep to avoid ingestion of gastro-intestinal nematodes associated with feces. *Anim. Sci.* **67**, 97–106. (doi:10.1017/S135772980009838)
 19. Smith LA, White PC, Marion G, Hutchings MR. 2008 Livestock grazing behavior and inter-versus intraspecific disease risk via the fecal–oral route. *Behav. Ecol.* **20**, 426–432. (doi:10.1093/beheco/arn143)
 20. Fleurance G, Duncan P, Fritz H, Cabaret J, Cortet J, Gordon IJ. 2007 Selection of feeding sites by horses at pasture: testing the anti-parasite theory. *Appl. Anim. Behav. Sci.* **108**, 288–301. (doi:10.1016/j.applanim.2006.11.019)
 21. Hutchings MR, Kyriazakis I, Papachristou TG, Gordon IJ, Jackson F. 2000 The herbivores' dilemma: trade-offs between nutrition and parasitism in foraging decisions. *Oecologia* **124**, 242–251. (doi:10.1007/s004420000)
 22. Bao J, Giller PS, Stakelum G. 1998 Selective grazing by dairy cows in the presence of dung and the defoliation of tall grass dung patches. *Anim. Sci.* **66**, 65–73. (doi:10.1017/S135772980008845)
 23. Cooper J, Gordon IJ, Pike AW. 2000 Strategies for the avoidance of faeces by grazing sheep. *Appl. Anim. Behav. Sci.* **69**, 15–33. (doi:10.1016/S0168-1591(00)00116-7)
 24. Garnick SW, Elgar MA, Beveridge I, Coulson G. 2010 Foraging efficiency and parasite risk in eastern grey kangaroos (*Macropus giganteus*). *Behav. Ecol.* **21**, 129–137. (doi:10.1093/beheco/arp162)
 25. Keymer AE, Read AF. 1991 Behavioural ecology; the impact of parasitism. In *Parasite–host associations: coexistence or conflict?* (eds CA Toft, A Aeschlimann, L Bolis), pp. 37–61. Oxford, UK: Oxford University Press.
 26. Gibbons LM. 2010 *Keys to the nematode parasites of vertebrates*. Supplementary volume. Wallington, UK: CAB International.
 27. Viggers KL, Lindenmayer DB, Cunningham RB, Donnelly CF. 1998 The effects of parasites on a wild population of the mountain brushtail possum (*Trichosurus caninus*) in south-eastern Australia. *Int. J. Parasitol.* **28**, 747–755. (doi:10.1016/S0020-7519(98)00022-8)
 28. Arundel JH, Beveridge I, Presidente PJA. 1979 Parasites and pathological findings in enclosed and free-ranging populations of *Macropus rufus* (Desmarest) (Marsupialia) at Menindee, New South Wales. *Aust. Wildl. Res.* **6**, 361–379. (doi:10.1071/WR9790361)
 29. Cripps J, Beveridge I, Ploeg R, Coulson G. 2014 Experimental manipulation reveals few subclinical impacts of a parasite community in juvenile kangaroos. *Int. J. Parasitol. Parasites Wildl.* **3**, 88–94. (doi:10.1016/j.ijppaw.2014.03.005)
 30. Cripps JK, Martin JK, Coulson G. 2016 Anthelmintic treatment does not change foraging strategies of female eastern grey kangaroos, *Macropus giganteus*. *PLoS ONE* **11**, e0147384. (doi:10.1371/journal.pone.0147384)
 31. Sharp JG, Garnick S, Elgar MA, Coulson G. 2015 Parasite and predator risk assessment: nuanced use of olfactory cues. *Proc. R. Soc. B* **282**, 20151941. (doi:10.1098/rspb.2015.1941)
 32. Murray DL, Cary JR, Keith LB. 1997 Interactive effects of sublethal nematodes and nutritional status on snowshoe hare vulnerability to predation. *J. Anim. Ecol.* **66**, 250–264. (doi:10.2307/6026)
 33. Murray DL, Keith LB, Cary JR. 1998 Do parasitism and nutritional status interact to affect production in snowshoe hares? *Ecology* **79**, 1209–1222. (doi:10.1890/0012-9658(1998)079%5B1209:DPANSI%5D2.0.CO;2)
 34. Gooderham K, Schulte-Hostedde A. 2011 Macroparasitism influences reproductive success in red squirrels (*Tamiasciurus hudsonicus*). *Behav. Ecol.* **22**, 1195–1200. (doi:10.1093/beheco/arr112)
 35. Fugazzola MC, Stancampiano L. 2012 Host social rank and parasites: plains zebra (*Equus quagga*) and intestinal helminths in Uganda. *Vet. Parasitol.* **188**, 115–119. (doi:10.1016/j.vetpar.2012.03.019)
 36. Arneberg P, Folstad I, Karter AJ. 1996 Gastrointestinal nematodes depress food intake in naturally infected reindeer. *Parasitology* **112**, 213–219. (doi:10.1017/S003118200008478X)
 37. Arneberg P, Folstad I. 1999 Predicting effects of naturally acquired abomasal nematode infections on growth rate and food intake in reindeer using serum pepsinogen levels. *J. Parasitol.* **85**, 367–369. (doi:10.2307/3285648)
 38. van der Wal R, Irvine J, Stien A, Shepherd N, Albon SD. 2000 Faecal avoidance and the risk of infection by nematodes in a natural population of reindeer. *Oecologia* **124**, 19–25. (doi:10.1007/s004420050)
 39. Irvine RJ, Corbishley H, Pilkington JG, Albon SD. 2006 Low-level parasitic worm burdens may reduce body condition in free-ranging red deer (*Cervus elaphus*). *Parasitology* **133**, 465–475. (doi:10.1017/S0031182006000606)
 40. Turner WC, Versfeld WD, Kilian JW, Getz WM. 2012 Synergistic effects of seasonal rainfall, parasites and demography on fluctuations in springbok body condition. *J. Anim. Ecol.* **81**, 58–69. (doi:10.1111/j.1365-2656.2011.01892.x)
 41. Ezenwa VO. 2004 Selective defecation and selective foraging: antiparasite behavior in wild ungulates? *Ethology* **110**, 851–862. (doi:10.1111/j.1439-0310.2004.01013.x)
 42. Worsley-Tonks KE, Ezenwa VO. 2015 Anthelmintic treatment affects behavioural time allocation in a free-ranging ungulate. *Anim. Behav.* **108**, 47–54. (doi:10.1016/j.anbehav.2015.07.018)
 43. Morgan ER, Shaikenov BS, Torgerson PR, Medley GF, Milner-Gulland EJ. 2005 Helminths of saiga antelope in Kazakhstan: implications for conservation and livestock production. *J. Wildl. Dis.* **41**, 149–162. (doi:10.7589/0090-3558-41.1.149)
 44. Ezenwa VO, Jolles AE. 2008 Horns honestly advertise parasite infection in male and female African buffalo. *Anim. Behav.* **75**, 2013–2021. (doi:10.1016/j.anbehav.2007.12.013)
 45. Budischak SA, Jolles AE, Ezenwa VO. 2012 Direct and indirect costs of co-infection in the wild: linking gastrointestinal parasite communities, host hematology, and immune function. *Int. J. Parasitol. Parasites Wildl.* **31**, 2–12. (doi:10.1016/j.ijppaw.2012.10.001)
 46. Apio A, Plath M, Wronski T. 2006 Localised defecation sites: a tactic to avoid re-infection by gastro-intestinal tract parasites in bushbuck, *Tragelaphus scriptus*? *J. Ethol.* **24**, 85–90. (doi:10.1007/s10164-005-0166-2)
 47. Brambilla A, von Hardenberg A, Kristo O, Bassano B, Bogliani G. 2013 Don't spit in the soup: faecal avoidance in foraging wild Alpine ibex, *Capra ibex*. *Anim. Behav.* **86**, 153–158. (doi:10.1016/j.anbehav.2013.05.006)
 48. Hutchings MR, Milner JM, Gordon IJ, Kyriazakis I, Jackson F. 2002 Grazing decisions of Soay sheep, *Ovis aries*, on St Kilda: a consequence of parasite distribution? *Oikos* **96**, 235–244. (doi:10.1034/j.1600-0706.2002.960205.x)
 49. Jones OR, Anderson RM, Pilkington JG. 2006 Parasite-induced anorexia in a free-ranging mammalian herbivore: an experimental test using Soay sheep. *Can. J. Zool.* **84**, 685–692. (doi:10.1139/z06-045)
 50. Craig BH, Tempest LJ, Pilkington JG, Pemberton JM. 2008 Metazoan–protozoan parasite co-infections and host body weight in St Kilda Soay sheep. *Parasitology* **135**, 433–441. (doi:10.1017/S0031182008004137)
 51. Fankhauser R, Galeffi C, Suter W. 2008 Dung avoidance as a possible mechanism in competition between wild and domestic ungulates: two experiments with chamois *Rupicapra rupicapra*. *Eur. J. Wildl. Res.* **54**, 88–94. (doi:10.1007/s10344-007-0115-1)
 52. McKenna PB. 1981 The diagnostic value and interpretation of faecal egg counts in sheep. *N. Z. Vet. J.* **29**, 129–132. (doi:10.1080/00480169.1981.34821)
 53. Seivwright LJ, Redpath SM, Mougeot F, Watt L, Hudson PJ. 2004 Faecal egg counts provide a reliable measure of *Trichostrongylus tenuis* intensities in free-living red grouse *Lagopus lagopus scoticus*. *J. Helminth.* **78**, 69–76. (doi:10.1079/JOH2003220)

54. Cripps J, Beveridge I, Martin JK, Borland D, Coulson G. 2015 Temporal dynamics of helminth infections in eastern grey kangaroos (*Macropus giganteus*) in Victoria. *Aust. J. Zool.* **63**, 163–174. (doi:10.1071/Z015003)
55. Shipley, B. 1999 Testing causal explanations in organismal biology: causation, correlation and structural equation modeling. *Oikos* **86**, 374–382. (doi:10.2307/3546455)
56. Hamel S, Côté SD, Gaillard JM, Festa-Bianchet M. 2009 Individual variation in reproductive costs of reproduction: high-quality females always do better. *J. Anim. Ecol.* **78**, 143–151. (doi:10.1111/j.1365-2656.2008.01459.x)
57. Pedersen AB, Fenton A. 2015 The role of antiparasite treatment experiments in assessing the impact of parasites on wildlife. *Trends Parasitol.* **31**, 200–211. (doi:10.1016/j.pt.2015.02.004)
58. Cripps J, Beveridge I, Coulson G. 2013 The efficacy of anthelmintic drugs against nematodes infecting free-ranging eastern grey kangaroos, *Macropus giganteus*. *J. Wildl. Dis.* **49**, 535–544. (doi:10.7589/2012-06-151)
59. Speare R, Skerratt LF, Berger L, Johnson PM. 2004 Toxic effects of mebendazole at high dose on the haematology of red-legged pademelons (*Thylogale stigmatica*). *Aust. Vet. J.* **82**, 300–303. (doi:10.1111/j.1751-0813.2004.tb12710.x)
60. Poppi DP, Sykes AR, Dynes RA. 1990 The effect of endoparasitism on host nutrition—the implications for nutrient manipulation. *Proc. New Zeal. Soc. An.* **50**, 237–243.
61. Lozano GA. 1991 Optimal foraging theory: a possible role for parasites. *Oikos* **60**, 391–395. (doi:10.2307/3545084)
62. Kyriazakis I, Tolkamp BJ, Hutchings MR. 1998 Towards a functional explanation for the occurrence of anorexia during parasitic infections. *Anim. Behav.* **56**, 265–274. (doi:10.1006/anbe.1998.0761)
63. Beldomenico PM, Begon M. 2010 Disease spread, susceptibility and infection intensity: vicious circles? *Trends Ecol. Evol.* **25**, 21–27. (doi:10.1016/j.tree.2009.06.015)
64. Anderson RC. 2000 *Nematode parasites of vertebrates: their development and transmission*, 2nd edn. Oxford, UK: CAB International.
65. Cripps JK, Wilson ME, Elgar MA, Coulson G. 2011 Experimental manipulation of fertility reveals potential lactation costs in a free-ranging marsupial. *Biol. Lett.* **7**, 859–862. (doi:10.1098/rsbl.2011.0526)
66. Aussavy M, Bernardin E, Corrigan A, Hufschmid J, Beveridge I. 2011 Helminth parasite communities in four species of sympatric macropodids in western Victoria. *Aust. Mammal.* **33**, 13–20. (doi:10.1071/AM10020)
67. Hutchings MR, Kyriazakis I, Gordon IJ, Jackson F. 1999 Trade-offs between nutrient intake and faecal avoidance in herbivore foraging decisions: the effect of animal parasitic status, level of feeding motivation and sward nitrogen content. *J. Anim. Ecol.* **68**, 310–323. (doi:10.1046/j.1365-2656.1999.00287.x)
68. Bordes F, Morand S. 2011 The impact of multiple infections on wild animal hosts: a review. *Infect. Ecol. Epidemiol.* **1**, 7346. (doi:10.3402/iee.v1i0.7346)
69. Clutton-Brock T, Sheldon BC. 2010 Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends Ecol. Evol.* **25**, 562–573. (doi:10.1016/j.tree.2010.08.002)
70. Raffel TR, Martin LB, Rohr JR. 2008 Parasites as predators: unifying natural enemy ecology. *Trends Ecol. Evol.* **23**, 610–618. (doi:10.1016/j.tree.2008.06.015)
71. Lima SL, Bednekoff PA. 1999 Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**, 649–659. (doi:10.1086/303202)
72. Ferrari MC, Sih A, Chivers DP. 2009 The paradox of risk allocation: a review and prospectus. *Anim. Behav.* **78**, 579–585. (doi:10.1016/j.anbehav.2009.05.034)
73. Laundré JW, Hernández L, Altendorf KB. 2001 Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. *Can. J. Zool.* **79**, 1401–1409. (doi:10.1139/z01-094)
74. Laundré JW, Hernández L, Rippele WJ. 2010 The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* **3**, 1–7. (doi:10.1139/cjz-79-8-1401)
75. Weinstein SB, Moura CW, Mendez JF, Lafferty KD. 2018 Fear of feces? Tradeoffs between disease risk and foraging drive animal activity around raccoon latrines. *Oikos* (doi:10.1111/oik.04866)
76. Brown JS. 1988 Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47. (doi:10.1007/BF00395696)
77. Hegglin D, Bontadina F, Gloor S, Romer J, Müller U, Breitenmoser U, Deplazes P. 2004 Baiting red foxes in an urban area: a camera trap study. *J. Wildl. Manage.* **68**, 1010–1017. (doi:10.2193/0022-541X(2004)068[1010:BRFIAU]2.0.CO;2)
78. Altendorf KB, Laundré JW, López González CA, Brown JS. 2001 Assessing effects of predation risk on foraging behavior of mule deer. *J. Mammal.* **82**, 430–439. (doi:10.1644/1545-1542(2001)082<0430:AEOPRO>2.0.CO;2)
79. Beringer J, Millsaugh JJ, Sartwell J, Woeck R. 2004 Real-time video recording of food selection by captive white-tailed deer. *Wildl. Soc. Bull.* **32**, 648–654. (doi:10.2193/0091-7648(2004)032<0648:RVROFS>2.0.CO;2)
80. Lavelle MJ, Hygnstrom SE, Hildreth AM, Campbell TA, Long DB, Hewitt DG, Beringer J, VerCauteren KC. 2012 Utility of improvised video-camera collars for collecting contact data from white-tailed deer: possibilities in disease transmission studies. *Wildl. Soc. Bull.* **36**, 828–834. (doi:10.1002/wsb.216)