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Fluctuations in field vole abundance indirectly influence red grouse productivity via a shared predator guild

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Changes in the abundance of one prey species may indirectly affect other prey species by triggering responses in generalist predators. Here we examine relationships between two prey species that do not compete directly, the field vole *Microtus agrestis*, a common rodent with fluctuating populations, and the red grouse *Lagopus lagopus scotica*, a gamebird inhabiting open moorland, during a 27-year study on a moor in south-west Scotland. First, we test whether vole abundance was related to grouse density and demographic rates. Second, we test whether vole abundance was related to abundance indices of four common predators of both voles and grouse (red fox *Vulpes vulpes*, weasel *Mustela nivalis*, hen harrier *Circus cyaneus* and common buzzard *Buteo buteo*). Third, we test whether these vole–grouse and vole–predator relationships differ in relation to grouse management, which includes the culling of foxes and weasels. We found no association between vole abundance and grouse densities, adult summer survival or nesting success. However, the ratio of young grouse per adult and the proportion of female grouse with broods in July were negatively associated with field vole abundance, suggesting increased predation of grouse chicks in years with high vole abundance. Fox indices showed a weak positive association with vole abundance when their numbers were not controlled, whilst weasel indices showed no relationship with voles. The numbers of breeding hen harriers and buzzards were also not associated with vole abundance, but the number of buzzard sightings was higher when voles were more plentiful. Our results are consistent with a negative interaction between field voles and red grouse chick survival in a pattern expected for apparent competition. Although the underlying mechanisms could not be disentangled, this interaction may be at least partly mediated by rodent-hunting raptors such as buzzards and, in periods without grouse management, foxes.

Keywords: aggregative numerical response, alternative prey hypothesis, apparent competition, incidental prey, predator–prey relationship

In ecological communities, indirect interactions between species mediated by a shared predator can play an important role in population dynamics (Wootton 1994). Changes in abundance of a preferred prey can trigger functional or numerical responses in generalist predators, which may in turn influence their predation rates on alternative prey (Selås 2001). The 'alternative prey hypothesis' predicts that predators switch to alternative prey when the abundance of their preferred prey is low (Angelstam et al. 1984, Nordberg and Schwarzkopf 2019), which can result in a positive relationship between the abundances of two prey species (Abrams and Matsuda 1996). Conversely, high abundance of preferred prey may lead to an aggregative response of predators and increased predation of incidental prey in the same habitat (Vickery et al. 1992, McKinnon et al. 2013), potentially generating an inverse relationship between the abundances of two prey species termed 'apparent competition' (Holt 1977, Holt and Kotler 1987). Hereby, the preferred prey negatively affects survival and abundance of the alternative prey, resembling the pattern generated by a direct competitive interaction.

The field vole *Microtus agrestis* is a common rodent in Britain and continental Europe. In many northern regions, field vole abundance fluctuates in three- to five-year cycles, which are thought to be driven mainly by extrinsic factors such as predation and food supply, although interactions with intrinsic factors may contribute to shaping their population dynamics (Korpimäki et al. 2004, Andreassen et al.

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2013). In Fennoscandia, variation in the relative impact of generalist and specialist predators on vole populations has been associated with the north–south gradient in vole cycle amplitude and length (Lambin et al. 2000). According to the 'predation hypothesis', specialist predators drive pronounced vole cycles in the north, whilst generalist predators, combined with higher abundance of alternative prey species, have a stabilising influence on vole populations in the south (see also Erlinge et al. 1984). However, this gradient does not appear to extend southwards to Britain and central Europe, where field vole populations can also show wide amplitude fluctuations, similar to those in central Fennoscandia, despite the prevalence of generalist predators (Lambin et al. 2000, 2006). As field voles are an important prey species (Dyczkowski and Yalden 1998), these abundance fluctuations can have a large impact on both predators and other prey species. Most previous studies, especially from arctic and boreal habitats, have found that predation of alternative prey, such as gamebirds, increased when vole abundance was low, supporting the alternative prey hypothesis (Marks-tröm et al. 1988, Leckie et al. 1998, Tornberg et al. 2012, Breisjøberget et al. 2018). In contrast, some studies from temperate forests, which support a more species-rich prey community, have found support for increased predation of alternative prey in years with high vole abundance. For example, Grendelmeier et al. (2018) found that incidental predation of wood warbler *Phylloscopus sibilatrix* nests by rodent-hunting mammals increased when rodent abundance was high, resulting in a negative interaction between wood warbler nest success and rodent abundance consistent with apparent competition. Similarly, Francksen et al. (2017) showed during a three-year study on diet and foraging patterns of common buzzards *Buteo buteo* that consumption of red grouse *Lagopus lagopus scotica* was highest in the peak year of vole abundance.

The red grouse is a gamebird of economic importance on heather moorland in large parts of the British uplands, which can also show quasi-cyclical fluctuations in abundance (Potts et al. 1984). There is no direct competition between voles and grouse for resources. Although both are herbivores, grouse feed on heather *Calluna vulgaris* and prefer heather-dominated areas, whereas voles feed on grasses and are more abundant in grass-dominated areas (Leckie et al. 1998, Wheeler 2005). However, the heterogeneous heather-grass mosaics found on many moors promote close spatial proximity between these species, which are both preyed upon by a shared guild of predators. Where moorland is managed for commercial grouse shooting, gamekeepers control a range of generalist predators and manage the balance and structure of the heather-grass mosaic (Hudson and Newborn 1995), which may influence predator–prey dynamics and predator-mediated interactions between voles and grouse, particularly in multi-predator systems.

Here, we examine relationships between field voles and red grouse in a 27-year study on a moor in southwest Scotland, which was subject to alternating periods with and without grouse management. Specifically, we wished to test whether grouse survival and productivity was positively or negatively associated with vole abundance. Similarly, we examined whether the abundance indices of four predators of both voles and grouse, i.e. red fox *Vulpes vulpes* and weasel *Mustela nivalis*, which were both controlled in managed periods, as well as hen harrier *Circus cyaneus* and buzzard, which were legally protected, were positively associated with vole abundance. Field voles can be an important prey for all four species; weasels are vole specialists (Tapper 1976), while fox, hen harrier and buzzard are generalist predators. Foxes and larger raptors are important predators of adult grouse (Hudson et al. 1997) and also take chicks and, in case of foxes, eggs. Locally, hen harriers can take significant numbers of grouse (especially chicks; Thirgood et al. 2000a), and whilst consumption of grouse by individual buzzards is low, their collective impact may be considerable if present in large numbers (Francksen et al. 2019). Weasels are less likely to take an adult grouse than stoats *Mustela erminea*, but, like stoats, may impact on grouse productivity by depredating eggs and chicks (Park et al. 2002).

To be consistent with the 'alternative prey hypothesis', we would expect positive grouse–vole and predator–vole associations. In contrast, negative grouse–vole interactions combined with positive predator–vole relationships would be consistent with the 'apparent competition hypothesis'. We further test whether these relationships differ with respect to grouse management. We expect fox and weasel indices to be associated with vole abundance only in periods when their numbers were not controlled, which may also have repercussions on grouse–vole relationships.

Methods

Study site and moorland management

The study was conducted between 1992 and 2018 on Langholm Moor in southwest Scotland (55°21′9″N, 2°88′5″W). The 115-km² site was dominated by a heterogeneous mosaic of heather and grass moorland (Fig. 1), which was surrounded by acid grassland (where heather previously dominated but had been lost through overgrazing by sheep, Thirgood et al. 2000b), interspersed with wooded stream gullies, agriculturally-improved grassland and patches of commercial coniferous forest and mixed deciduous woodland (Ludwig et al. 2018a).

Smaller vole-eating raptors such as kestrel *Falco tinnunculus* and owls were not monitored systematically and were thus not considered here. We also did not consider raptors that mainly hunt birds (peregrine *Falco peregrinus*, goshawk *Accipiter gentilis*, merlin *Falco columbarius*, sparrowhawk *Accipiter nisus*) as they are not directly affected by fluctuations in vole abundance, or corvids (raven *Corvus corax*, carrion crow *Corvus corone*). Although corvids can prey on both grouse and voles and may impact on grouse productivity (Parker 1984), they are opportunistic omnivores who often feed on carrion (Cramp and Simmons 1984) and thus are also unlikely to be affected by fluctuations in vole abundance (Norrdahl and Korpimäki 2002).

During the study, Langholm Moor was subject to alternating periods when the moor was managed for red grouse (1992–1999 and 2008–2016; Ludwig et al. 2017) and when it was not (2000–2007 and 2017–2018). However, grouse were last shot in 1996, and harvest only contributed to overwinter grouse mortality during the first five years of

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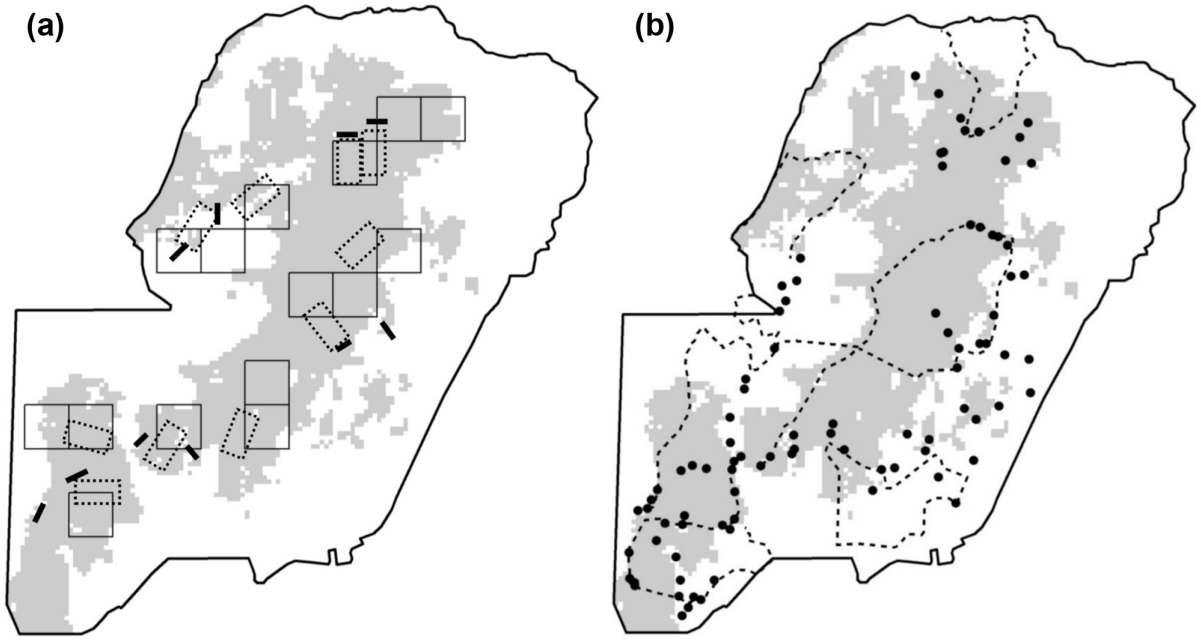


Figure 1. Distribution of survey areas on Langholm Moor, (a) 0.5-km² grouse count blocks (dotted lines), vole trap lines (thick lines) and 1-km² Breeding Bird Survey squares (thin lines), (b) fox scat transects (dotted lines) and mustelid footprint tunnels (circles). The extent of heather moorland is shaded grey.

this 27-year study. When managed for grouse, five gamekeepers controlled foxes, carrion crows, weasels and stoats on the whole 115-km² site, and managed the heather habitat by controlled burning and, from 2008 onwards, cutting to promote fresh heather growth for grouse and to increase vegetation heterogeneity. Simultaneously, the moor was used for sheep farming, which became the primary land-use between 2000 and 2007, when the moor was not managed for grouse (Baines et al. 2008). Following five decades of heavy sheep grazing, which converted almost half of the heather moorland to acid grassland (Thirgood et al. 2000b), sheep grazing ceased in 2011 on 39 km² of moorland to facilitate heather restoration (Ludwig et al. 2018a).

Red grouse counts

Grouse were counted annually in March and July (with the exception of March 1992 and 2001) on ten 0.5 km² blocks of representative moorland habitat (Fig. 1a), two in each of the five 'beats' managed by gamekeepers, to obtain pre- and post-breeding densities (total number of birds counted km^{-2}, Redpath and Thirgood 1999). Within each count block, the observer walked parallel transects 150 m apart (mean transect length per block: 3.3 ± 0.2 km), while a pointing dog quartered the ground on either side of the transect searching for grouse. Birds counted in July were aged as young or adult by size and plumage characteristics and used to calculate two measures of annual grouse productivity; the proportion of females with broods (broods female^{-1}) and the ratio of young per adult (young adult^{-1}). We estimated nesting success, i.e. the proportion of clutches where ≥ 1 chick hatched, from 119 first clutches of radio-tagged females in 2009–2016 (for details see Ludwig et al. 2018b). Annual rates of 'adult summer survival' were estimated as post-breeding adult density/pre-breeding density.

Field vole abundance

Vole abundance was estimated annually between late March and early April at ten locations on heather moorland/acid grassland habitat (Fig. 1a), two in each 'beat' as above. At each location, 50 unbaited snap traps were set over two nights, giving a total of up to 1000 'trap nights' per annum (Redpath et al. 1995). Traps were checked after the first night, any individuals caught removed and the trap reset. Sprung but empty or faulty traps were excluded from the total number of trap nights. Overall, field voles comprised 73% of all small mammals caught (n = 916). Other species caught were common shrew *Sorex araneus* (18%), wood mouse *Apodemus sylvaticus* (7%) and pygmy shrew *Sorex minutus* (2%). The total number of field voles (summed across all trap locations) caught per 100 trap nights was used as an index of annual vole abundance. To assess within-year changes in vole indices, we also estimated indices in late June/early July on a subsample of six out of the original ten locations in 2012–2015. Density estimates from snap-trapping closely resembled those from live-trapping elsewhere (Korpimäki and Norrdahl 1991).

Abundance of predators of field voles and red grouse

From 2003 onwards, an index of red fox activity was estimated annually from repeat surveys of scat transects (Fig. 1b; 2003–2007: three transects, 2008–2010: five transects, 2011–2016: six transects, 2017–2018: three transects). Each transect, running along linear features such as walls and fences, was approximately 10 km long and surveyed up to four times. The first observer in March removed all scats and up to three repeat surveys were conducted at monthly intervals. Transects were surveyed on foot, and scanned within 2 m either side of the transect, all scats encountered were

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removed. To account for variation in transect length and interval between consecutive surveys, the total number of scats found during the repeat surveys (summed across transects), excluding those from the clear-up round, was divided by total transect length and the exposure period in days (i.e. the time interval between the clear-up round and the final visit). The fox index was then presented as the total number of scats km^{-1} 10 $days^{-1}$.

Between 2002 and 2015, we also estimated small mustelid (stoat and weasel) activity in late April/early May from footprint tunnel tracking (Graham 2002). We set either 50 (2002–2007) or 75 tunnels (2008–2015) per annum for 14 days at locations likely to be used by stoats and weasels (Fig. 1b; King and Edgar 1977), and calculated the proportion of tunnels with mustelid footprints. Because 99% of the tunnels with footprints (n = 117) were identified as weasel, this was used as an index of weasel abundance. We could not estimate an index of stoat abundance, because there were too few detections of stoat footprints. Generally, stoats were less abundant than weasels as gamekeepers annually removed an average of 181 ± 24 weasels (2008–2015), but only 72 ± 11 stoats.

The number of breeding hen harrier females was recorded annually by observing birds displaying, nest-building, transporting prey or performing food passes (Hardey et al. 2013, Ludwig et al. 2017). All nests were on moorland habitat. In 1993 and from 2008 onwards, we also recorded the number of active buzzard nests by observing birds displaying and searching suitable habitat for nesting (Graham et al. 1995, Francksen et al. 2017), which included wooded stream gullies and patches of forest.

As nest-based monitoring for buzzards was restricted across years and varied in relation to search effort, we also obtained abundance indices of buzzard and hen harrier from annual surveys of breeding birds within 15 1-km grid squares on moorland habitat (1992–2018), three located in each of the five 'beats' (Fig. 1a). Between 1992 and 2002, squares were surveyed once between late-May and mid-July (only 12 squares were surveyed in 1997 and 2001, and 14 in 1998). From 2003 onwards, all squares were surveyed twice following Harris et al. (2018), in mid-April to mid-May, and then in mid-May to mid-June. Within each square, the observer walked along two parallel 1-km transects, separated by 500 m, recording birds seen or heard. We used the maximum count from the two survey visits (summed across all squares) and calculated annual abundance indices as the total number of sightings km^{-1} to account for variation in the number of squares counted.

Data analysis

All analyses were conducted at the level of the study site owing to insufficient spatial overlap between the monitoring units of the different species, i.e. surveys of predators were not associated with survey plots of grouse and voles (Fig. 1). Thus, we has a single value of each measure for the whole study site for each year. We defined 'grouse management' as a factor with two levels (managed: 1992–1999 and 2008–2016; unmanaged: 2000–2007 and 2017–2018). However, as the collection of predator indices and pre-breeding grouse densities in 2008 commenced before predator control was effective, the respective indices in that year were assigned to the unmanaged period (managed: 1992–1999 and 2009–2016; unmanaged: 2000–2008 and 2017–2018).

To analyse the relationship between vole abundance and grouse densities or demographic rates, we used a series of generalized linear models (GLM). Each grouse measure was included, in turn, as response variable, with the vole index, 'grouse management' and their interaction as explanatory variables (Table 1). The interaction term allowed us to test whether the relationship between grouse demographic measures and vole index differed between periods of different management, and was removed from the model if non-significant. As grouse survival has previously been shown to be density-dependent (Thirgood et al. 2000a), adult summer survival was analysed by using the log-transformed post-breeding density of adult grouse as response variable and including the log-transformed pre-breeding density as additional covariate in the model.

To test whether the abundance of common predators of voles and grouse was related to vole abundance, we used a series of GLMs as above, with each predator measure, in turn, as response variable and the vole index, 'grouse management ' and their interaction (which was removed if non-significant) as explanatory variables (Table 1).

As all data were time series, we tested the residuals in all models for first-order serial autocorrelation using the

Table 1. Structure of generalized linear models used to analyse relationships between grouse/predator variables and vole index and grouse management. Initial models also included the interaction between the vole index and grouse management, which was removed when not significant.

Variable	Error term	Response variable	Explanatory variables
Grouse pre-breeding density	normal	ln(pre-breeding density)	Vole index + Grouse management
Grouse post-breeding density	normal	ln(post-breeding density)	Vole index + Grouse management
Grouse adult survival	normal	ln(post-breeding density)	Vole index + Grouse management + ln(pre-breeding density)
Grouse young adult^{-1}	Poisson	n young, offset by ln(n adults)	Vole index + Grouse management
Grouse broods female^{-1}	binomial	n females with broods, binomial totals = n females	Vole index + Grouse management
Grouse nesting success	binomial	n successful clutches, binomial totals = n clutches	Vole index + Grouse management
Fox index	Poisson	n scats, offset by ln(km × days/10)	Vole index + Grouse management
Weasel index	binomial	n tunnels with footprints, binomial totals = n tunnels	Vole index + Grouse management
Hen harrier breeding females	Poisson	n breeding females	Vole index + Grouse management
Buzzard breeding pairs	Poisson	n breeding pairs	Vole index + Grouse management
Hen harrier sightings	Poisson	n sightings, offset by ln(km)	Vole index + Grouse management
Buzzard sightings	Poisson	n sightings, offset by ln(km)	Vole index + Grouse management

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Durbin–Watson test and, in case of an inconclusive result, the Wooldridge test (Wooldridge 2012). The only residuals showing significant autocorrelation were those obtained from the analysis of breeding hen harrier females, which we then reanalysed using the log-transformed number of breeding females as response variable and explanatory variables as above in a linear regression with correlated normal errors. Statistical analysis were conducted in GenStat 19.1 (VSN International 2018), and models were adjusted for over-dispersion when necessary.

Results

Field vole abundance in spring generally fluctuated in 3–4-year intervals at Langholm, with the amplitude between population highs and lows nearly doubling in the two intervals during the second managed period (Fig. 2a). Additional summer trapping of voles on a subsample of locations in four years indicated that the annual index of vole abundance (measured in late March/early April) does not necessarily reflect vole abundance in July, when post-breeding grouse counts were conducted. Vole abundance decreased between April and July by 71% and 84% in 2012 and 2015, whereas it increased by 32% and 33% in 2013 and 2014.

We found no relationship between spring vole abundance and grouse densities, adult summer survival or nesting success (Table 2), but the ratio of young per adult and the proportion of females with broods in July were negatively associated with vole abundance in spring (see also Fig. 2a, 3). All measures of grouse densities, survival and reproductive performance were positively associated with grouse management (Table 2), and there were no significant interactions between vole abundance and grouse management.

The relationship between fox indices and spring vole abundance varied in relation to grouse management (Table 3, Fig. 2b). Fox indices were weakly positively associated with vole abundance in unmanaged years (0.17 ± 0.07, $F_{1,6} = 6.10$, $p = 0.048$), but not in managed years (-0.09 ± 0.09, $F_{1,6} = 0.96$, $p = 0.365$), when the fox index was significantly lower (Fig. 3). However, the effect of grouse management far outweighed the effect of voles (Table 3). Weasel indices were neither related to vole abundance nor to grouse management.

The numbers of breeding hen harriers and buzzards were not associated with spring vole abundance or grouse management (Table 3, Fig. 2c). This result did not change when the harrier model was corrected for serial autocorrelation (vole abundance: 0.10 ± 0.06, $t = 1.71$, $p = 0.100$, management: -0.001 ± 0.367, $t = 0.00$, $p = 0.998$). However, buzzard sightings during breeding bird surveys increased with vole abundance, whereas sightings of harriers did not (Fig. 2d, 3). Harrier sightings during surveys were positively correlated with breeding numbers ($r_s = 0.64$, $n = 27$, $p<0.001$), but the same was not significant for buzzards ($r_s = 0.35$, $n = 12$, $p = 0.069$).

Discussion

High field vole abundance was associated with lower red grouse productivity and higher abundance of some generalist predators (red fox and buzzard). The direction of these relationships is consistent with predictions from the 'apparent competition hypothesis' but not with those from the 'alternative prey hypothesis' (i.e. higher grouse productivity in peak vole years). Vole abundance was unrelated to grouse densities, adult summer survival or nesting success, suggesting an indirect negative interaction between voles and grouse chick survival. However, our measure of vole abundance was from spring and limited repeat sampling of voles in July, when grouse productivity was measured, showed inconsistent patterns.

Studies on vole–grouse interactions in the boreal zone of Fennoscandia have found that abundance and productivity of forest grouse fluctuate positively and synchronously with vole populations (Angelstam et al. 1985, Lindström et al. 1987, Markström et al. 1988, Tornberg et al. 2012, Breisjøberget et al. 2018). These patterns support the 'alternative prey hypothesis'. However, our study system on a managed grouse moor was located in the temperate zone, where vole population fluctuations are generally less pronounced and both predator and prey communities more diverse (Lambin et al. 2000). Hence, changes in vole abundance may have a weaker effect on predator populations, and other processes may have greater influence on predator–prey dynamics (Angelstam et al. 1985). Our study site was periodically subject to intensive control of foxes, small mustelids, which can otherwise collectively affect ground-nesting bird density and productivity (Parker 1984, Fletcher et al. 2010, Ludwig et al. 2017). For example, between 2008 and 2015, gamekeepers annually removed an average of 189 foxes, 72 stoats and 181 weasels (Ludwig et al. 2019). Removing a range of predator species is likely to have changed the relative importance of other predators and their effect on grouse–vole interactions.

Elsewhere in Europe, foxes, stoats and weasels are known to respond numerically to changes in vole abundance (Lindström 1989, Korpimäki et al. 1991). In our study, fox indices showed a weak, positive relationship with vole abundance only when the moor was not managed for grouse and foxes were not controlled while our weasel index showed no relationship. Our method of assessing mustelid indices proved unsuitable for stoats, which were rarely recorded despite being regularly killed by the gamekeepers. Accordingly, we could not consider the relationships between voles, grouse and stoats, which elsewhere have a larger relative impact on grouse than weasels (Park et al. 2002). Hen harrier breeding density was positively influenced by vole abundance only in the earlier years of this study (Redpath et al. 2002; Fig. 1c), but within the entire 27-year timeseries the two measures were unrelated. This suggests that recruitment of hen harriers may have been influenced by other factors, for example large-scale variation in the abundance of other prey such as meadow pipits *Anthus pratensis* (Redpath and Thirgood 1999) and grouse (Baines and Richardson 2013), or high rates of illegal culling of hen harriers elsewhere (Etheridge et al. 1997, Murgatroyd et al. 2019). As the number of hen harriers observed during the breeding bird surveys was also unrelated to vole abundance, it seems unlikely that hen harriers were mediating the observed grouse–vole interaction.

Buzzard breeding density did not correlate with vole abundance. However, the number of buzzard sightings

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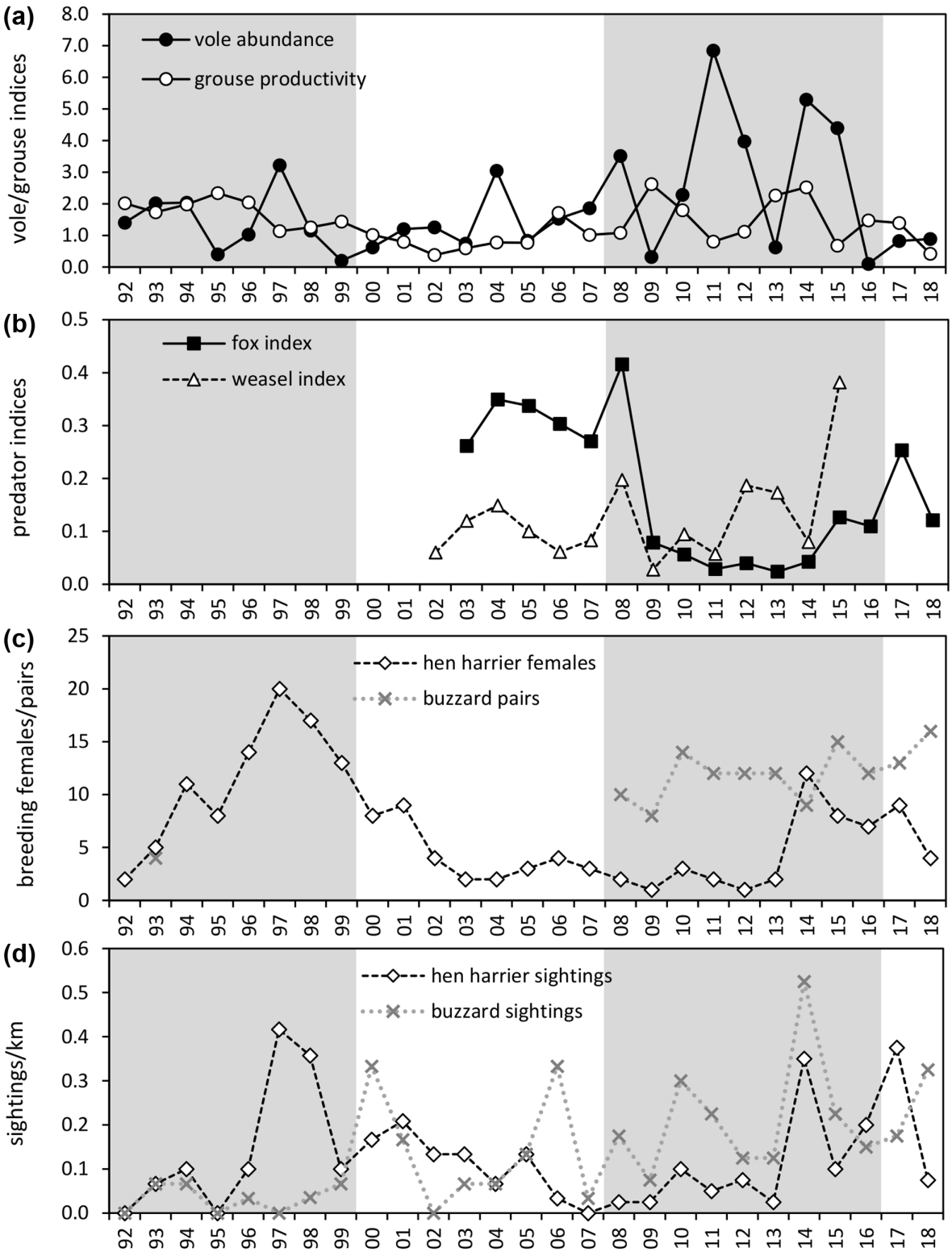


Figure 2. Annual indices of (a) field vole abundance (voles 100 trap nights^{-1}) and red grouse productivity (young adult^{-1}), (b) mammalian predator abundance (fox: scats/km/day×10; weasel: proportion of tunnels with footprints), (c) number of breeding hen harriers and buzzards and d) hen harrier and buzzards sighting rates during breeding bird surveys, on Langholm Moor between 1992 and 2018. Periods of active grouse moor management (1992–1999 and 2008–2016) are highlighted in grey (note that predator abundance indices in 2008 were assigned to the unmanaged period for analyses). Foxes and weasels were culled when the moor was managed for grouse, whilst raptors were protected in all years.

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Table 2. Relationship between annual indices of field vole abundance in spring, grouse management and red grouse densities or demographic rates in the same year. Values are parameter estimates ± SE (reference level for grouse management = 'unmanaged'), and p-values of <0.05 are highlighted in bold. Non-significant interaction terms were removed from the final models.

Grouse variables	Vole abundance	Grouse management	Interaction term
Pre-breeding density	0.04 ± 0.03, $F_{1,22}$ = 1.24, p = 0.278	0.70 ± 0.12, $F_{1,22}$ = 34.32, **p < 0.001**	$F_{1,21}$ = 1.62, p = 0.217
Post-breeding density	0.03 ± 0.04, $F_{1,24}$ = 0.51, p = 0.482	0.86 ± 0.14, $F_{1,24}$ = 40.38, **p < 0.001**	$F_{1,23}$ = 0.74, p = 0.399
Adult summer survival	0.01 ± 0.02, $F_{1,22}$ = 0.24, p = 0.630	0.16 ± 0.08, $F_{1,22}$ = 4.73, **p = 0.041**	$F_{1,21}$ = 0.01, p = 0.923
Young adult^{-1}	−0.10 ± 0.04, $F_{1,24}$ = 6.22, **p = 0.020**	0.69 ± 0.21, $F_{1,24}$ = 11.17, **p = 0.003**	$F_{1,23}$ = 0.15, p = 0.699
Broods female^{-1}	−0.19 ± 0.08, $F_{1,24}$ = 6.53, **p = 0.017**	1.27 ± 0.33, $F_{1,24}$ = 15.21, **p < 0.001**	$F_{1,23}$ = 0.37, p = 0.551
Nesting success	−0.15 ± 0.11, $F_{1,6}$ = 1.85, p = 0.223	–	–

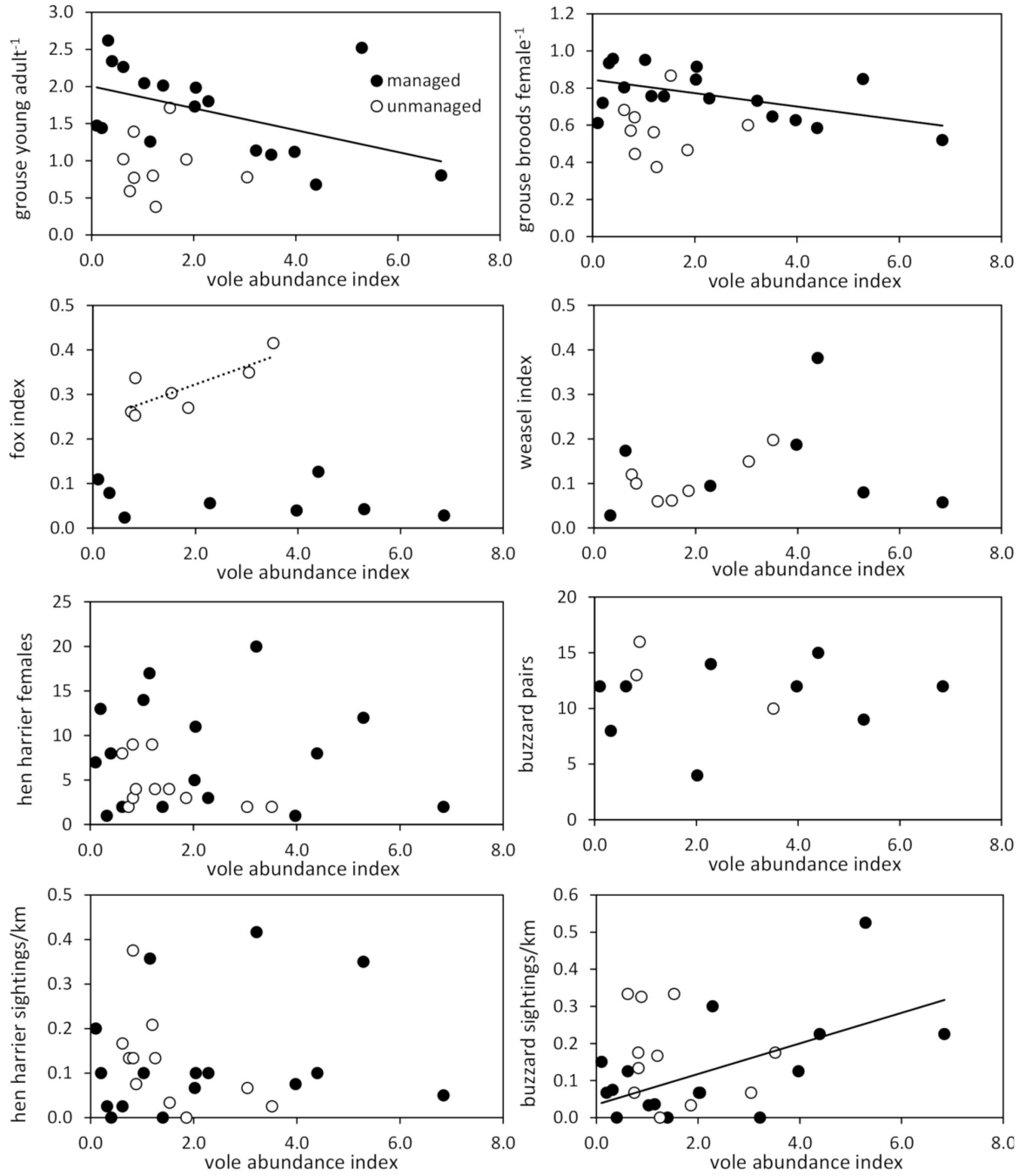


Figure 3. Relationships between field vole abundance (voles 100 trap nights^{-1}) and indices of red grouse productivity, abundance of mammalian predators (fox index: scats/km/day × 10; weasel index: proportion of tunnels with footprints) and abundance of raptors in managed (filled circles) and unmanaged (open circles) periods. Trend lines are only shown for significant relationships (solid line: overall relationship irrespective of management; dotted line: relationship during unmanaged years only).

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Table 3. Relationship between annual indices of field vole abundance, grouse management and relative abundance indices of predators of voles and grouse. Values are parameter estimates ± SE (reference level for grouse management = 'unmanaged'), and p-values of <0.05 are highlighted in bold. Foxes and weasels were culled as part of grouse management, but not hen harrier and buzzard.

Predator variables	Vole abundance	Grouse management	Interaction term
Fox index	0.03 ± 0.07, $F_{1,13}$ = 0.16, p = 0.700[#]	−1.65 ± 0.25, $F_{1,13}$ = 43.52, **p < 0.001**	$F_{1,12}$ = 5.03, **p = 0.045**
Weasel index	0.08 ± 0.12, $F_{1,11}$ = 0.44, p = 0.521	0.14 ± 0.50, $F_{1,11}$ = 0.08, p = 0.783	$F_{1,10}$ = 0.67, p = 0.432
Hen harrier breeding females	−0.05 ± 0.09, $F_{1,24}$ = 0.37, p = 0.550	0.58 ± 0.32, $F_{1,24}$ = 3.24, p = 0.084	$F_{1,23}$ = 0.94, p = 0.343
Hen harrier sightings	0.04 ± 0.11, $F_{1,24}$ = 0.14, p = 0.709	−0.05 ± 0.39, $F_{1,24}$ = 0.01, p = 0.910	$F_{1,23}$ = 2.91, p = 0.102
Buzzard breeding pairs	0.01 ± 0.05, $F_{1,9}$ = 0.04, p = 0.844	−0.19 ± 0.22, $F_{1,9}$ = 0.76, p = 0.406	$F_{1,8}$ = 1.07, p = 0.330
Buzzard sightings	0.21 ± 0.09, $F_{1,24}$ = 5.13, **p = 0.033**	−0.44 ± 0.36, $F_{1,24}$ = 1.50, p = 0.233	$F_{1,23}$ = 1.97, p = 0.174

[#] unmanaged: 0.17 ± 0.07, $F_{1,6}$ = 6.10, **p = 0.048**; managed: −0.09 ± 0.09, $F_{1,6}$ = 0.96, p = 0.365.

during breeding bird surveys was higher in vole peak years, and could possibly be explained by breeding birds shifting their foraging areas from vole-poor farmland habitats to vole-rich heather moorland (Francksen et al. 2017). In contrast to hen harriers, which breed in relative isolation on Langholm Moor (in most years the nearest known other breeding pair was >20 km away), the buzzard population is more contiguous, with birds breeding locally and in the surrounding landscape. Francksen et al. (2017) found that increased buzzard hunting intensity on moorland habitat during a vole peak year coincided with higher consumption of red grouse. Similarly, Selås (2001) showed that incidental predation of adders *Vipera berus* by buzzards increased in vole peak years, when adders were also attracted to vole-rich habitat. The buzzard–vole relationship may thus at least partly explain the negative interaction between vole abundance and grouse productivity. However, incidental predation of grouse chicks by other rodent specialists such as stoats (Park et al. 2002) or short-eared owls *Asio flammeus* (Roberts and Bowman 1986), which were not included in the analyses, may have also contributed to this pattern.

At Langholm, voles did not exhibit a dampening of amplitude fluctuations as recently seen both in a nearby forest (Millon et al. 2014) and in other temperate regions across Europe (Cornulier et al. 2013). Alternatively, the amplitude of fluctuations approximately doubled during the second period of grouse management, which may have been associated with changes in livestock grazing (Villar et al. 2014, Evans et al. 2015). Elsewhere, this may influence rodent-hunting predators (Wheeler 2008, Villar et al. 2013), but we only found an increase in buzzard sightings, not breeding pairs and fox indices, the latter only when foxes were not controlled by gamekeepers.

Our study was subject to several limitations, and the results thus need to be interpreted with caution. Grouse productivity was negatively related to vole abundance, but the mechanisms driving this interaction remain unclear due to the four-month delay between measuring vole abundance (March) and grouse productivity (July). Most grouse chicks hatch in late May, and any impact on chick survival will occur during the latter half of these four months. Our results show that vole abundance changes between March and July. The vole population may crash or recover within the grouse breeding period (see also Lambin et al. 2000, Redpath et al. 2002), and some predators may be able to respond quickly to these within-season changes in vole abundance. In a multi-predator community, different mechanisms may also interfere with each other. For example, while some predators may reduce their predation of grouse in vole peak years (alternative prey hypothesis), as suggested for foxes (Leckie et al. 1998), others, such as buzzards, may aggregate and thus increase incidental predation on grouse (apparent competition), possibly counteracting their respective effects on grouse and weakening any grouse–vole relationships. Finally, our data on predator abundance were incomplete; foxes and mustelids were only monitored during the latter half of the study period, and we had no information on annual abundance of other potential predators of both voles and grouse, such as stoat and short-eared owl. To fully disentangle the underlying mechanisms would require repeated breeding season surveys of voles and all predators (including their diets).

The patterns observed in our study did not fit the predictions of the 'alternative prey hypothesis', but were consistent with those of the 'apparent competition hypothesis'. However, the observational nature and limitations of our study necessitate some limitation in our inference, and while our data tended to support the apparent competition hypothesis, they did not allow us to conclusively reject the alternative prey hypothesis. Future work with replicated sites or a before–after control impact study design could more fully differentiate between the two hypotheses and disentangle the potentially interacting mechanisms within a multi-predator community.

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