Hen harrier foraging success in relation to land use in Scotland

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Abstract
In the UK, hen harriers (Circus cyaneus) are illegally killed on moorland that is managed for red grouse (Lagopus lagopus scoticus), and they produce fewer young per female on grouse moorland than on either unmanaged moorland or forestry. However, those breeding attempts on grouse moorland that escape nest destruction produce more young than in other land-use classes. One explanation for this difference is that food is more available to harriers on managed moorland than elsewhere. To examine this hypothesis, we compared the capture rates of hunting male harriers on sites across Scotland. Four of these sites were managed for grouse whilst the remaining three consisted of either unmanaged moorland or a mixture of unmanaged moorland and young forestry plantations. We found a significant difference in capture rates, with harriers on managed grouse moorland capturing prey at a greater rate than elsewhere, supporting the idea that prey were more available on grouse moorland. However, there was no difference in strike rates between the land-use classes, suggesting that prey were not necessarily more abundant on grouse moors. Males on unmanaged moorland tended to catch larger prey, though this was insufficient to compensate fully for the reduced capture rates. The improved hunting success on grouse moorland means that this habitat is likely to be more attractive to breeding harriers, thereby increasing the conflict between those interested in maximizing grouse numbers and those interested in conserving rare raptors.

INTRODUCTION
The conflict between those who wish to maximize gamebird numbers for hunting and those who seek to protect raptor populations is an important issue in conservation today (Kenward, 1999). Raptors are often seen as direct competitors for a limited resource and are illegally killed as a consequence. In the UK, hen harriers (Circus cyaneus) are scarce, protected raptors, yet they are still illegally killed on moorland that is managed for red grouse (Lagopus lagopus scoticus). The extent of this persecution is such that harrier breeding success, abundance and distribution are all adversely affected (Bibby & Etheridge, 1993; Etheridge, Summers & Green, 1997; Green & Etheridge, 1999). There is evidence, however, that in the absence of persecution these managed moors would provide optimal breeding habitat for harriers in the UK. Clutch size and the average number of young fledged from successful hen harrier nests on managed grouse moorland are significantly greater than in other land-use categories (Etheridge et al., 1997, Green & Etheridge, 1999). In this paper we consider why managed moorland might be ideal breeding habitat for harriers and what the implications are for conservation and land management.

The aim of grouse management is to maximize the number of grouse available for shooting in the autumn (Hudson & Newborn, 1995). To achieve this, gamekeepers are employed to control predators and to manage the vegetation through burning. In the absence of illegal persecution, this management may benefit hen harriers in two main ways. First, some prey species and in particular red grouse may be more abundant on managed moorland (Tharme et al., 2001) and may also be more available to harriers. Second, within geographical regions, the numbers of potential predators of harriers are likely to be lower on managed moors (Hudson, 1992; Tharme et al., 2001) so predation of harrier clutches or broods may also be lower in this land-use type. Here we focus on the hypothesis that prey are more available to harriers on grouse moorland.

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Deriving estimates of prey abundance for predators that hunt a wide variety of prey types in a variety of habitat types is problematic. Different prey types require different techniques to estimate their abundance and the biases inherent in counting techniques will vary according to the structure of the habitat (Bibby & Buckland, 1987; Bibby, Burgess & Hill, 1992). Also, counts of prey do not necessarily give a measure of prey availability, as this will also vary with vegetation structure (Simmons, 2000). In this paper we attempt to overcome these problems by examining the foraging behaviour of hen harriers during the breeding season in a number of upland areas. We predict that if prey are more abundant on managed moorland, then the rate at which harriers strike at prey when hunting these sites should be higher. In addition, if prey are more available to harriers on managed moorland, then we predict that the rate at which prey are captured by hunting harriers should be higher. Grouse chicks are an important prey of harriers on managed moorland (Picozzi, 1978; Redpath, 1991; Redpath & Thirgood, 1997), so we considered whether the differences observed in hunting patterns between land-use classes could be accounted for solely by differences in grouse chick availability.

The prediction that strike rates will be higher where prey are abundant depends on the assumption that strike rates simply reflect prey abundance. However, it is possible that predators may become more selective about which individuals they attack as abundance increases, in which case strike rates may not increase with prey abundance, but the percentage of strikes that lead to captures will increase. As strikes at grouse chicks can be distinguished from strikes at other prey (Redpath, 1992), we examined the strike rate at grouse chicks and the probability of grouse capture in relation to the abundance of grouse chicks. Lastly we considered how birds might compensate on sites where capture rates are reduced.

METHODS

Study areas

Seven sites were used in the study: one each in mainland Argyll, referred to as Argyll hereafter (1992–94), Islay (1992–94), Dumfries-shire (1993–2000), Inverness-shire (1986–87) and Orkney (1998–2000), and two sites in Perthshire (1988 and 1995) (Fig. 1). Sites in Dumfries-shire, Inverness-shire and Perthshire comprised heather moorland managed for grouse, and were characterized by heather-dominant \textit{(Calluna vulgaris)} vegetation with a mosaic of burnt patches. Argyll, Islay and Orkney sites consisted of unmanaged moorland used for grazing sheep \textit{(Oves aries)}, with no burning and more grassland-dominated areas. Sites in Argyll and Islay also had areas of commercial forestry plantations of varying age, and hunting in this land use was distinguished from hunting in unmanaged moorland.

Hunting behaviour

Foraging observations were made within each area in conditions of good visibility from vantage points. Within study areas, observations were spread throughout the breeding season (from May to July inclusive). Individual
male harriers were selected as they flew into view and observed until they were lost from sight or ceased foraging. From knowledge of local nest sites and observations of individuals carrying prey back to nests, we were confident that in all cases several individual male harriers hunted these areas. Flight behaviour that was clearly not aimed at detecting prey (e.g., territorial display, agonistic interactions and prey transit) was excluded, as were harriers flying >10 m (approximately) above the ground. A tape recorder, set to run continuously for the duration of each foraging bout, was used to record the time and the number of prey strike attempts and successful captures. One potential bias in our study was that different observers worked in separate sites. However, strikes and captures were relatively unambiguous and were recorded in the same way by all of us. Strike attempts were defined as those strikes where the bird landed on the ground. Multiple strikes, apparently at the same prey individual or brood, were considered to be a single strike. Captures were usually obvious from the harrier’s subsequent behaviour. Failed strikes were generally followed by the immediate resumption of foraging, whereas captures resulted in harriers at least partially plucking prey at or near the capture site then either eating the prey or flying with it to the nest. In the few cases where the outcome was unclear, strike sites were searched for evidence of prey capture (e.g., plucked feathers, fur and viscera). Because adult grouse vigorously defend their young, we were able to distinguish between strikes at grouse chicks and at other prey (Redpath, 1992). Strikes at grouse were also recorded on an ad hoc basis during the course of fieldwork as well as during hunting observations, and all strikes by male harriers were included when considering how the percentage of successful strikes varied with grouse abundance.

Grouse chick abundance

On all managed moors the abundance of grouse chicks in early June was assessed using pointing dogs (Redpath, 1992; Redpath & Thirgood, 1999). Grouse did occur on all other sites, but at very low density, and were not counted. Grouse abundance was compared first to the rate at which harriers struck at grouse chicks and second to the percentage of those strikes that were successful. In 2 years (1998 and 1999) no strikes at grouse chicks were observed on the Dumfries-shire site, so analyses were done including and excluding these years. As grouse chick abundance varied considerably between years, we have taken each year as a separate point, giving a sample size of 10 (8 excluding 1998 and 1999).

Prey weights

Hides were erected near harrier nests on five of the study sites (no data from Inverness-shire and Argyll). For each site we counted the number of prey items delivered by males during the first 4 weeks of the nestling period and estimated the prey weights (see Redpath & Thirgood, 1999; Redpath et al., 2001). These data were used to determine the average weight of prey for each site.

Statistical analysis

Analyses were done in Minitab (v11) and SAS (v6.12). To examine variation in strike and capture rates in relation to land use (forestry, unmanaged moorland and managed moorland), we used generalized linear mixed models (GLMMs) with both year and site included in models as random terms in the model to control for the non-independence of observations on the same site in different years. Each observation bout was the sample unit in these analyses. To model the strikes and captures as rates per unit time we used the number of strikes or captures as a dependent variable with Poisson error and log link and used the log of the duration of the observation bout (in seconds) as an offset. This is equivalent to modelling strike or capture rates as log-linear functions of independent variables. The models were implemented using a GLIMMIX macro in SAS (Littel et al., 1996). Denominator degrees of freedom were calculated in SAS using Satterthwaite’s formula (Littel et al., 1996). All subsequent pair-wise comparisons were conducted in the GLIMMIX models, through t-tests of the differences in least square means (DLSM).

RESULTS

Over the course of 16 years we recorded 49.6 hours of male hunting, in which time 436 strikes at prey and 136 prey captures were observed (Table 1). Similar amounts of hunting data were obtained from managed (25.9 hrs and 258 strikes) and unmanaged sites (23.7 hrs and 178 strikes).

Capture rates varied significantly with land use (Fig. 2; $F_{2,12} = 6.8$, $P = 0.01$). Hunting harriers caught prey more frequently on managed moorland than on either the unmanaged moorland sites (DLSM $P = 0.006$) or the forestry sites (DLSM $P = 0.04$). Orkney had the lowest capture rate of any of the sites (Table 1), with harriers capturing 0.9 items per hour compared to between 1.8 and 4.9 items per hour elsewhere. Excluding Orkney data, the pattern in capture rates was maintained although the overall difference was not quite statistically significant ($F_{2,14} = 3.4$, $P = 0.06$). However, the difference between managed and unmanaged moorland was still significant (DLSM $P = 0.03$).

There was no significant difference in the rate at which male harriers struck at prey in relation to land use (Fig. 2; $F_{2,8} = 1.6$, $P = 0.26$). There were also no significant differences in any of the pair-wise comparisons. So, although capture rates were higher on managed moorland this pattern was not reflected in strike rates.

Attacks on grouse broods were only seen on the managed sites (Table 1). Nevertheless, even excluding those observations during which grouse captures occurred, capture rates still differed significantly with land use ($F_{2,10} = 4.4$, $P = 0.04$), with a significant difference between managed and unmanaged moorland (DLSM $P = 0.02$). In other words, the difference in capture rates
between land uses could not just be explained by the availability of grouse chicks. During hunting observations, 30 strikes at grouse were observed. In addition, a further five strikes were seen on managed moors during periods of other fieldwork. There was a significant linear relationship between strike rate at grouse chicks and grouse chick abundance (including all data: $r = 0.64, N = 10, P = 0.04$; excluding zeros: $r = 0.87, N = 8, P = 0.005$). However, there was no relationship between the percentage of strikes that were successful and grouse chick abundance ($r = 0.44, N = 8, P = 0.3$). This suggests that, at least for grouse, strike rate but not capture probability reflected abundance.

Males delivered 1882 items during watches at 40 nests (Table 1). There were considerable differences between sites and the average weight of prey delivered to nests on unmanaged sites was $78 \pm 10$ g compared to $46 \pm 15$ g on managed sites. Combining these data with capture rates gave an estimate of the biomass caught per hour hunting and suggested that males hunting unmanaged sites caught $118 \pm 56$ g per hour compared to $162 \pm 78$ g on managed sites. So, even controlling for differences in biomass, males on managed sites caught food at a greater rate.

### DISCUSSION

Harriers captured prey more readily on managed moorland than on unmanaged moorland or forestry, providing support for the hypothesis that prey are more available on grouse moors than elsewhere. Grouse broods were only seen to be attacked on managed moorland, but even excluding these observations, harriers also caught other prey more frequently in this land-use category.

Why might prey be more available on grouse moors? The most obvious explanation is that harrier prey are actually more abundant on managed sites. Because harriers take many prey types and the structure of the vegetation differed between land-use types, we were unable to derive a single comparable measure of prey abundance across areas to compare with hunting patterns. Nevertheless, our results show that strike rates were similar on managed and unmanaged sites. This suggests either that prey abundance did not vary in relation to management or that strike rates reflect changes in the behaviour of hunting harriers, such that individuals hunting sites with lots of prey may be more selective about which prey they attack, whereas those on prey-poor sites may be forced to strike at any prey, however unlikely the probability of capture. The idea that strike rates reflect abundance rather than changes in hunting behaviour was supported by the finding that strike rates at grouse chicks increased with abundance whereas the probability of capture did not. Another line of evidence is that two other studies have examined the abundance of some potential prey species on managed and unmanaged moorland in northern England and the Scottish highlands (Etheridge et al., 1997; Tharme et al., 2001).
They found that, apart from grous chicks, important prey such as meadow pipits (*Anthus pratensis*) and skylarks (*Alauda arvensis*) are either as abundant or less abundant on managed moorland. In our study, unmanaged sites were geographically distinct from managed sites with more grass-dominated vegetation, so species such as meadow pipits and voles (*Microtus* spp.) may actually be more abundant on these unmanaged sites (Redpath & Thirgood, 1997; Smith et al., 2001). We conclude that it is unlikely that harrier prey other than grouse were more abundant on our managed sites, but comparative estimates of abundance of the main prey species on the different sites are necessary to test this idea.

Alternative explanations for the variation in prey availability between sites are that either the vegetation structure or the behaviour of harriers or the behaviour of their prey influences capture rate. Harriers selectively hunt the edges of burnt patches (Redpath, 1992), so habitat mosaics resulting from heather burning may provide better capture opportunities for harriers. Within one site (Dumfries-shire) we found no evidence that habitat characteristics influenced the likelihood of capture (Redpath & Thirgood, 1997), although the variation in habitat between sites may be much greater than within a site. Madders (2000) has suggested that strike success may be dependent on habitat heterogeneity, with birds on unmanaged sites hunting a wider variety of habitat types and using less specialized and therefore less successful techniques. Alternatively, capture rates may reflect the age and experience of the birds. However, the fact that harriers on grouse moors tend to be younger than elsewhere, because of persecution, suggests that this explanation is unlikely (Etheridge et al., 1997). Lastly, the behaviour of the prey may influence capture rates. Prey exposed to more predators may alter their behaviour so making them less vulnerable (Lima & Dill, 1989). It may therefore be harder for harriers to catch prey on unmanaged moorland where they may be exposed to higher densities of predators. The pattern in capture rates across land-use classes may therefore be dependent on differences in prey abundance, vegetation structure, prey behaviour or predator behaviour. Measurements of these variables and experimental manipulations are now necessary to distinguish between the most important factors influencing prey availability.

Harriers on Orkney had the lowest capture rates of all the sites in this study. This is an area where harrier numbers are currently declining (Meek et al., 1998) and where food appears to be an important limiting factor (Amar & Redpath, 2002). Our data on hunting behaviour provided some support for the idea that food is less available for hen harriers on Orkney than elsewhere and may be contributing to the poor breeding performance and population decline.

Males tended to catch larger prey on unmanaged sites, suggesting that they may be able to compensate partially for the reduced capture rates during hunting. Although we only had data from five sites, there were considerable differences in average prey size, with prey on unmanaged sites being roughly 30 g larger. Despite this, we estimated that male harriers on managed moorland still caught on average 53 g more prey per hour of hunting than males on unmanaged sites. This assumed that all items were completely eaten by harriers, whereas in reality only small prey were totally consumed, so the difference between the amount of food caught per hour was probably even greater on managed sites.

The data for this study come from only seven study sites that are geographically distinct. Ideally, of course, it would be better to have data from more sites and in particular from neighbouring areas that differed in land use. Nevertheless, our data do provide some support for the idea that harriers may be more productive on grouse moors because prey are more available there. Unfortunately, this finding means that harriers may be attracted to breed on grouse moors where they subsequently suffer high levels of human interference (Etheridge et al., 1997). Indeed, a recent survey of harriers in the UK found that the majority of the breeding population is now found on grouse moors (Sim et al., 2001). Heather moorland has been declining since the 1940s, especially away from areas that are managed for grouse (Robertson, Park & Barton, 2001). This loss of heather and concurrent reductions in the amount of forestry habitat suitable for breeding harriers means that the proportion of harriers attempting to breed on managed grouse moors is likely to increase (Redpath et al., 1997; Madders, 2000). As predation by harriers can adversely affect the economics of grouse shooting (Redpath & Thirgood, 1999; Thirgood et al., 2000a, c), this shift to grouse moors is likely to intensify the conflict between conservation organizations and grouse moor owners (Thirgood et al., 2000b). An understanding of the factors that are important in making prey less available on unmanaged grouse moors would therefore be greatly beneficial for the future conservation of this species in Britain. If the effects of reduced prey availability can be mitigated, more harriers may breed on unmanaged sites, thereby decreasing the proportion of the British population that comes into conflict with game interests.

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