Using PIT tag technology to target supplementary feeding studies

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Abstract

The role of food in limiting or regulating populations of mammalian herbivores remains a central question in ecology with great relevance to wildlife and livestock management. Supplementary feeding studies have been widely used to assess the potentially limiting role of food availability and supplementary feeding is also a common management technique. In both contexts there is an assumption that all individuals in the target population have access to food. There are, however, questions as to whether supplementary feed reaches the target population and how benefits are translated into individual and population level effects. We describe and use a technique using Passive Induced Transponder (PIT) tags to monitor individual use of supplementary feed in wild mountain hare populations and test the assumption that supplementary feed reaches the target population. Over the course of one winter only 50% of the target hare population used supplementary feed and there was considerable individual variation in the time spent feeding among those individuals that fed. Neither age, sex nor an index of body condition were significant in explaining which individuals visited feeding stations or how long individuals spent feeding. The method and results described here suggest that, at least for the mountain hare, the central assumption that all target individuals have access to and use supplementary feed is invalid. Great care is thus needed in designing and interpreting the results of supplementary feeding studies or management programmes that include supplementary feeding.

Introduction

Identifying the factors that limit vertebrate populations is a central question in ecology and critical to the management and conservation of wild populations (Krebs 2002). While there is little doubt that food is ultimately limiting for most vertebrates, other proximate factors may limit population growth before food becomes a limiting factor. The role of food availability as a driver of vertebrate population dynamics remains unclear, primarily because of the difficulties in isolating the impacts of food from other confounding factors (Boutin 1990, Isaac et al. 2004, Wirsing & Murray 2007). Supplementary feeding experiments, where individuals or populations are provided with additional food, have been widely used to study the effects of food on vertebrate population dynamics, demography and behaviour (Karels et al. 2000, Predavec 2000, Thomas & Cuthill 2002, Boonstra & Krebs 2006, Boutin et al. 2006). The use of supplementary food by wild vertebrates is also a widely used technique in wildlife management, particularly to increase animal numbers, density, or local distribution (Hoodless et al. 1999, Putman & Staines 2004, Gonzalez et al. 2006).

Despite the proliferation of supplementary feeding studies, there is little consensus on the role of food availability in vertebrate population dynamics. In a review of 138 studies, Boutin (1990) found that while supplementary feeding had been associated with an increase in population density, earlier breeding, higher birth mass, greater juvenile survival and increased growth rates, overall the results of food-addition experiments had been inconclusive. Furthermore, while there was evidence that many populations were food limited, food addition alone failed to alter the population dynamics in any of the studies reviewed. A number of hypotheses have been suggested to account for the inconclusiveness of food addition studies (Boutin 1990, Wirsing & Murray 2007): (i) factors other than food become limiting after an increase in density; (ii) even though food is provided *ad libitum*, it becomes limiting after an increase in density because the way it is distributed does not allow all individuals access; (iii) the true response to food addition is less than the observed increase because most of the increase is due to immigration; (iv) food addition studies have not been conducted over large enough periods or areas to have much impact at the population level.

While behavioural studies employing food addition typically use the individual as the study unit (e.g. Thomas & Cuthill 2002), most studies that have investigated the role of food in population dynamics have assessed the effects of food addition at the population level (Boutin 1990). These studies have only considered the average response of the population and have not investigated how behavioural interactions between individuals over food affect how resources are partitioned, how food addition affects individual behaviour, or how the effects of supplementary feeding translate into individual life-history parameters (Dobson & Kjelgaard 1985, Boutin 1990, Klenner & Krebs 1991, Isaac et al. 2004). Concentrating on population level effects is a short-coming of many supplementary feeding experiments as behavioural factors may act to concentrate the effects of food shortage on certain individuals (Clutton-Brock & Albon 1985). Furthermore, few studies have assessed individual variation in the use of supplementary food and generally assume that all individuals have access to and use the food equally (but see: Isaac et al. 2004, Kenward et al. 2005). The logistical difficulty of assessing individual responses to supplementary food, particularly for cryptic or nocturnal species, has almost certainly contributed to the inconclusiveness of supplementary feeding studies.

Passive Induced Transponders

Passive Induced Transponders (PIT) tags consist of an electronic microchip encased in biocompatible glass, are typically 10-25 mm in length and 2-4 mm in diameter, and have been widely used in fisheries and wildlife research to assess habitat use (Greenberg & Giller 2001), movements (Harper & Batzli 1996), feeding behaviour (Isaac et al. 2004, Kenward et al. 2005) and individual life histories (Becker & Wendeln 1997). The application of PIT tags in wildlife research is reviewed by Gibbons & Andrews (2004). The tags are passive in that the tag is dormant until activated by a reader. If a tag is present the reader generates a close-range, electromagnetic field that causes the tag to transmit a unique alphanumeric code, which is read and stored by the reader. PIT tags are typically injected or surgically implanted into the animal necessitating the use of small tags and consequently limiting read range.

Population dynamics in mountain hares

Through out their range mountain hare *Lepus timidus* populations show regular large fluctuations in density; in particular Scottish mountain hare populations associated with moorland managed for red grouse *Lagopus lagopus scoticus* shooting show regular high amplitude fluctuations in density with a mean 9-year periodicity (Newey et al. 2007). The reasons for these dynamics remain unclear and our current work is investigating the affects of nutrition and parasites on mountain hare population dynamics (Newey & Thirgood 2004, Newey et al. 2005).

Faced with the challenge of assessing individual use of supplementary feed we developed a simple, robust, automated technique to monitor individual use of supplementary food using PIT tag technology. Here we describe the system used and present results on individual variation in use of supplementary feed.

Methods

The study was undertaken on two private estates managed for red grouse shooting in the Central Highlands of Scotland. The experimental design consisted of four study areas, two on each of the estates, each measuring 500 x 500 m. Hares on two of the study areas, one on each estate, were provisioned at feeding stations. These comprised a covered trough equipped with a sensor array (with three sensors per array) along each side of the trough, a reader-data logger (6-channel HDX Multi-point Decoder) and a 26 Ah, 12 v sealed lead acid (SLA) battery (Wyre Micro Designs Ltd, Lancashire, UK). The other two study areas served as controls. Mountain hares in Scotland have ranges of 10-12 ha (Hulbert et al. 1996, Rao et al. 2003) which equates to a circular area of radius 180–190 m. Four feeding stations per fed study area were spaced 200 m apart giving all hares in each study area access to at least one feeding station. Study areas were >1 km from each other to minimise movement between fed and control areas.

Hares were live-trapped in cages and long-nets between September and December 2005. Traps were placed throughout each study area on active hare runs, baited with apple and set at dusk, and checked at first light the following day. Each hare was sexed, aged (juvenile or adult), weighed and fitted with a small uniquely numbered ear-tag (Monel #1, National Band & Tag Co., Kentucky, USA). 119 hares were equipped with a collar-mounted 23 x 4 mm Half Duplex (HDX) PIT tag (Texas Instruments Inc., USA). The use of large externally mounted HDX tags used in this study provided a read range of 4-5 cm ensuring that feeding hares were detected, and at the same time reduced power consumption, allowing one battery to power two sensor arrays, reader and data logger for 8-9 days. 48 of the 119 PIT-tagged hares (Table 1) were also equipped with collar-mounted radio-transmitters (TW3, Biotrack Ltd, UK). From September 2005 until the end of the study in July 2006, radio-collared hares were located fortnightly to monitor survival and to assess possible movement between study areas. Hares were also live-trapped from March-July 2006.

Feeding stations were replenished with commercial rabbit chow and rolled oats coated with molasses weekly from September 2005 to April 2006. The PIT tag reader fitted to each feeding station polled each sensor every second and logged the presence of any PIT tag along with date and time. Once a PIT tag was detected by the reader its presence was initially logged every 20 seconds, but due to the high usage of the feeding stations and the initially limited data storage capacity (1,024 entries, this was subsequently increased to > 7,000 by using a larger memory module), data were logged at 60 second intervals for the majority of the study. The data were downloaded weekly to a handheld computer.

Assessing body condition of live animals under field conditions is difficult and the subject of considerable debate on the validity of different measures and indices (Krebs & Singleton 1993, Green 2001, Schulte-Hostedde et al. 2001, Schulte-Hostedde et al. 2005). Here we use the residuals of a linear regression of body mass against body size indexed by hind foot length as an index of body condition. While this method has been criticised (Green 2001), more recent assessment suggests that the residuals from a standard regression of body mass:size represent a valid index of body condition (Schulte-Hostedde et al. 2001, Schulte-Hostedde et al. 2005).

Statistical analysis was conducted in R 2.7.0 (R Development Core Team 2007) following Crawley (2005). The effects of age, sex and body condition on whether individuals used feeding stations or not, and the time individuals spent feeding were assessed using Generalised Linear Models (GLM). Age, sex and body condition index were included in the full model which was then subject to backwards stepwise deletion of the least non-significant terms until only the significant terms remained in the model. There were only two replicates of each treatment, therefore prohibiting the use of random effects models or any meaningful analysis of interaction terms. Study site (i.e. replicate) was therefore included in each analysis as a fixed factor and retained in the model as a “nuisance” variable during model selection, and the analysis was confined to assessing the main effects only.

Those animals that had been logged at a feeding station at least once during the study were classified as having used supplementary feed. We used a GLM with a binomial error term and logit link to assess the effects of sex, age and body condition index on whether or not animals used feeding stations.

The distribution of the total time each animal spent feeding was highly over dispersed, where the variance greatly exceeded the mean. Consequently to examine the effects of age, sex and body condition on the total time individuals were recorded at a feeding station we used a negative binomial GLM (Venables & Ripley 1997). To allow for the staggered entry of PIT tagged individuals into the study and for the death or loss of individuals we used the natural logarithm of the number of weeks an animal was known to be present on a fed site as an offset in the model, thereby essentially analysing the mean weekly time spent feeding. Where there was no telemetry or trapping data to confirm whether an individual was present and alive, we took the last date an animal was recorded at a feeding station to be the last known date to be alive and rounded this up to the nearest whole week.

Results

Of the 70 PIT tagged hares released on the two areas with supplementary feed, 35 (50%) visited a feeding station at least once (Table 1). In addition, two hares from control sites visited a feeding station indicating that there was movement between areas despite the distance between the sites (Table 1). These two animals, along with two animals with missing morphometric data, were excluded from the analyses. On both fed study areas, 50% of both adult and juvenile PIT-tagged males used feeding stations, whereas adult females were consistently more likely to use feeding stations than were juvenile females (Figure 1a). However neither age, sex or body condition index had any significant effect on whether individual hares used supplementary feed (sex; $X^2_1 = 0.004$, $p > 0.95$, body condition index;

$X^2_1 = 0.383$, $p > 0.54$, age; $X^2_1 = 0.259$, $p > 0.61$). There was considerable individual and site variation in the time animals were logged at feeding stations (Fig. 1b). Again, neither age, sex or body condition index had any significant effect on time spent feeding (sex; log-ratio = 0.07, df = 1,29, p = 0.79, age; log-ratio = 0.60, df= 1,30, p = 0.44, body condition index; log-ratio = 0.57, df = 1,31, p = 0.45).

Discussion

Supplementary feeding experiments have been widely used to investigate the role of food in limiting vertebrate populations on the assumption that food addition will increase survival and/or fecundity. However, despite the proliferation of such studies, the role of food availability in vertebrate population dynamics remains unclear. Supplementary feeding experiments have been criticised at a number of levels – in particular the question of whether supplementary feed actually reaches the target population and the difficulty of relating both population and individual responses directly to food addition (Boutin 1990, Wirsing & Murray 2007). The PIT tag system described here offers a simple, robust and automated method to assess individual use and potentially the individual-level effects of food supplementation and quantifies the proportion of a target population that actually used supplementary feed. The results of this study on mountain hares demonstrate that only a subset of the target population uses the food and that there is large individual variation in the use of food, reinforcing concerns voiced by Boutin (1990) and Wirsing & Murray (2007) and highlighting the importance of understanding food supplementation at the individual level.

We found no evidence for any significant role of sex, age or body condition in explaining why only half of the PIT-tagged hares used supplementary feed. Based on published range sizes of Scottish mountain hares (Hulbert et al. 1996, Rao et al. 2003), feeding stations were spaced 200 m apart to ensure that each hare's range included at least one feeder. Given that some individuals may have been trapped at the edge of their range, the observation that only half of the PIT tagged hares used feeding stations suggests that some hares either did not find, were prevented from, or chose not to use feeders. Some hares used more than one feeder on a study plot which, along with the observation that two PIT tagged hares from the control plots also found and used feeders, suggests that hare ranging behaviour was greater than previously described, hares were able to find feeders even if located outside of their presumed core range, and finally that hares were not averse to using feeders. The use of feeding stations may have been influenced by the position of the feeder relative to an individual's home range. The radio-telemetry data collected in this study did not allow a meaningful assessment of this hypothesis and we suggest future work should assess the effect of feeder placement relative to home range on feeder use through radio-telemetry or by increasing feeder density. There is no evidence that mountain hares are territorial or defend resources, and the PIT data show instances of two animals feeding simultaneously at the same feeder (unpublished data), and thus social exclusion seems unlikely but cannot be ruled out and warrants investigation.

Home range sizes of mountain hares and snowshoe hares are correlated with food availability (Boutin 1984, Hulbert et al. 1996) which supports the hypothesis that hares forage to minimise risk (Boonstra et al. 1998, Murray 2002). Individual hares that had adequate resources in their home range may have been averse to the risk of using novel resources such as artificial feeding stations. However, without detailed data on forage quality within each hare's home range this remains speculation and there is considerable potential for further work exploring habitat correlates with use of supplementary feed.

Given the large variation in the time individuals spent using feeding stations it is perhaps not surprising our analysis failed to identify any significant explanatory variables. The results do however suggest that some individual trait other than age, sex or body condition is more important in determining time spent feeding. Abundance and quality of browse in individual home ranges may account for the individual variation in the time spent at feeding stations. Differences in habitat quality between the two sites may also explain why individuals on site two appear to use feeders more than those on site one; we are however unable to explore this question further in the current study. There is however also a growing awareness that animal personality, which refers to consistent individual differences in behaviour, may play an important role in wild vertebrates influencing among other things boldness and ranging behaviour (Sih et al. 2004, Boon et al. 2007). This could explain why some individuals did not use feeders and the variation in time spent feeding.

In summary, we have described a simple, robust, affordable and practical system to monitor the individual use of supplementary food in vertebrates, and in the mountain hare system at least have demonstrated that there is considerable individual variation in the use of supplementary food. At present this variation cannot be explained by age, sex, or body condition. The occurrence of such individual variation means that the common assumption that supplementary feed reaches the entire target population is questionable, requiring care to be exercised in the design and interpretation of supplementary feeding experiments and supplementary feeding programmes for wildlife management and conservation.

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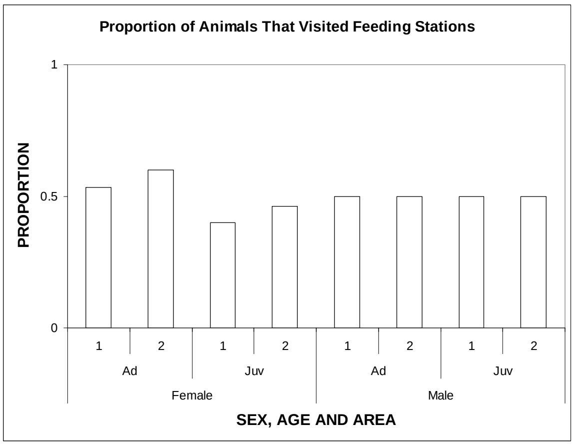
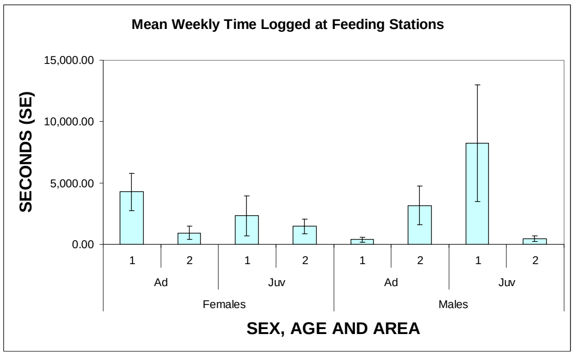
Table 1.

Area	No. Individuals PIT tagged (radio-collared)	No. Individuals using feeders (%)	Total visits	Total time (seconds)
Control 1	28 (13)	1* (3%)	474	42,698
Control 2	21 (8)	1* (5%)	39	2,602
Fed 1	36** (13)	18*** (50%)	11,422	1,154,933
Fed 2	34 (14)	17 (50%)	4,625	606,678
Total	119 (48)			





Legends & footnote for Table 1

Table 1. Details of the number of individuals fitted with PIT tags and radio collars in each study area along with total number of visits and time spent at feeding stations.

* Not included in analysis

** Two animals excluded from analysis due to missing data

*** One animal excluded from analysis due to missing data

Legend for Figure 1 (A and B)

Figure 1A. Proportion of PIT-tagged animals that visited feeding stations by sex, age and study area. 1 & 2 – study sites, Ad. – adult, Juv. – juvenile.

Figure 1B. Mean weekly and SE of time logged at feeding stations by sex, age, and study area. 1 & 2 – study sites, Ad. – adult, Juv. – juvenile.