The fate of released captive-reared grey partridges Perdix perdix: implications for reintroduction programmes

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The fate of released captive-reared grey partridges *Perdix perdix*: implications for reintroduction programmes

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We investigated the potential for released captive-reared grey partridges *Perdix perdix* to restock regions from which the species has disappeared. Birds were released at two sites in Scotland (not concurrently) from 1997 to 2003 and monitored via spring and autumn counts, night-time surveys and radio-telemetry. Some wild female partridges were caught and radio-tagged each spring for comparison with reared females. The survival rate of 520 captive-reared birds released in autumn until the following spring was poor (around 10% overall) and was not significantly different for radio-tagged and visibly-marked birds. Carrying a radiotag did not alter the body condition of the birds. The breeding-season survival rate of released hens averaged 30% and was not significantly different to that of 44% for wild hens. However, the power to detect significant differences was low due to the small number of survivors. The major cause of mortality throughout was predation (82 and 55% of losses at the two sites), with red foxes *Vulpes vulpes* and raptors being the most significant predators. Reared partridges at the study site with legal predator control had higher survival rates than those at the other site, but this was not true for wild hens as raptor predation compensated for declining mammalian predation rates (19% of deaths were due to raptors at the site without predator control, 56% at the site with predator control). We suggest that the vulnerability to predation of reared birds was most likely due to inappropriate antipredator behaviour or an increased risk of predation near to release pens. Of the partridges that survived long enough to breed, three times more wild hens reached incubation than reared hens. No reared hens raised chicks in their first breeding season whilst the only hen that survived long enough to breed in her second year raised 14 young. Captive-reared grey partridges could not be used to increase the species' range unless 1) the number surviving their first year increased, 2) the higher breeding rate of two-year-old females suggested here was ubiquitous, and unless 3) appropriate management was in place first. Methods for improving the success of releases are discussed.

Key words: body condition, predation, radio-telemetry, restocking, survival, wild and reared

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The grey partridge *Perdix perdix* has declined in number and range across the UK and much of Europe (Potts 1986, Gibbons et al. 1993, Tucker & Heath 1994, Burfield & van Bommel 2004) and is now absent from many areas previously occupied. Part of the UK Biodiversity Action Plan for this species is to enhance the current range. This might be achievable by improving the management of land at the edge of the current range to encourage expansion, as the species responds well to sympathetic management where present (e.g. Sotherton 1991, Tapper et al. 1996, Aebischer & Ewald 2004). However, changes in land management may not always be possible, especially where suitable patches are isolated, as partridges generally disperse over short distances (Potts 1986). A complementary option would be to reintroduce the species. It might be possible to translocate wild birds, but this would be possible only on a small scale and at a few locations at a time, because of the scarcity of 'surplus' wild birds.

The grey partridge is easily bred in captivity and is commercially reared to provide supplementary birds for shooting, but little is known about the fate of such birds after release. Radio-telemetry is a proven means of gathering such information from galliforms (e.g. grey partridge: Carroll 1990; red grouse *Lagopus lagopus scoticus*: Thirgood et al. 1998; ring-necked pheasant *Phasianus colchicus*: Leif 1994; black grouse *Tetrao tetrix*: Warren & Baines 2002), but a crucial part of any such study is to verify that the tagging of individuals does not affect them. This paper addresses the following questions with a view to investigating the suitability of commercially-reared birds for re-stocking: 1) Does radio-tagging have a negative impact on the tagged individuals?; 2) What is the survival rate of male and female captive-reared birds from release in autumn to the following spring?; 3) What is the survival rate of reared females through the summer and how does this compare to local wild females?; 4) What are the causes of mortality for released birds and how do these compare with wild partridges?; 5) What proportion of surviving birds goes on to breed?; 6) Is there a difference in the body condition of radio-tagged and un-tagged reared hens in the spring, and how does this compare to wild hens?

Material and methods

Study sites

From autumn 1997 to summer 2001, studies were conducted on approximately 10 km^2 of farmland near Arbroath, Angus, in the UK (56°37'N, 2°30'W). From autumn 2001 until summer 2004, studies switched to a site of similar area near Kirriemuir, Angus (56°38'N, 3°05'W). Both sites were characteristic of lowland agricultural habitats in Angus and were dominated by cereal production with some grass, oilseed rape *Brassica napus* and potatoes *Solanum tuberosum* grown. Both sites had natural-regeneration set-aside, with some game crops (predominantly kale *B. napus*, artichoke *Helianthus tuberosa*, mustard *Sinapis* spp. and triticale *Triticosecale*) in all years. Both sites had small woods (mixed deciduous and coniferous species, or commercial coniferous stands) and both had mostly dry-stone walls or wire fences as field boundaries, with few hedges or tree-lined boundaries. Grain feeders were provided at both sites in woods where pheasants were released and in some game crops. A full-time professional gamekeeper was present at Kirriemuir, overseeing a programme of legal predator control, whilst the Arbroath site was keepered on a part-time basis. Grey partridges were not deliberately shot at the sites.

Reared partridges

Eight-week old commercially-reared grey partridges (Heart of England Farms, Warwickshire, UK) were put into release pens in September each year of the study in groups of 14-20 to acclimatise to local conditions. No attempt was made to sex birds to minimise handling time. Pens were situated in or near cover (such as game crops) where possible to give protection from predators after release. After two or three weeks in the pens, birds were released a few individuals at a time during fine weather. Whilst some birds were held in the pens, released birds remained nearby. This facilitated familiarisation with the immediate vicinity and was intended to decrease the likelihood of them leaving the study area.

Impact of radiotags

The effect of radiotags on survival and body condition of the individuals carrying them was assessed experimentally. Dummy radiotags were fitted to some birds released during 2000-2003 to increase the number of birds carrying some kind of radiotag. These were tags that no longer emitted a signal.

From late February to early April each year, sites were searched at night to locate reared birds with and without a working or dummy radiotag (radio-telemetry was not used to locate tagged individuals during searches). This method allowed for an accurate identification of tagged and untagged birds because they were approached to within at least two metres. All suitable fields were searched systematically by foot using a powerful lamp. From 2001, a hand-held infra-red camera (FLIR systems, Kent, UK) was also used, which detected the body heat of roosting pairs at up to about 80 m. The lamp was used to 'hold' birds found and then a long-handled net was used to catch them so that wild and reared females could also be radio-tagged (if necessary).

Survival rates

Individual survival rates were estimated via radio-telemetry and from resightings of birds fitted with collars. A sample of birds was radio-tagged in most years when they were transferred to the release pens, or re-caught in the pens and tagged later during fine weather. Thus all tagged reared-birds had a period in the release pens to become accustomed to their radio-tag. The tags used were all backpack-mounted and either Biotrack (Dorset, UK; used in 1997 & 1998) or Holohil tags (Ontario, Canada; 2000-2004). The former weighed approximately 10 g and the latter 9 g (with mounts). This was 2.6 and 2.3%, respectively, of the body weight of the smallest bird weighed. All reared birds were also fitted with plastic-coated fabric collars (including radio-tagged birds) so that observers could distinguish them visually from wild birds (except in 1997, when all reared birds were radio-tagged), so all reared birds were handled in a similar way, with tagged birds handled for a few minutes longer than untagged birds.

Radio-tagged birds were located every 1-5 days to monitor their survival and breeding activity. All birds, i.e. wild and reared, with and without tags, were counted in March-April and in September-October by scanning fields with binoculars or driving across stubble fields (mostly present in the autumn) over the whole study area (up to approximately two kilometres from release pens). It was not always possible to distinguish tagged and untagged birds during these counts. The maximum distance moved by reared birds from the release pen detected by radio-tracking was approximately 2.5 kilometres (at Kirriemuir). This was just off the main study area, so it was outwith the area surveyed for collared birds. The maximum distance moved detected for collared birds was about 1.5 km. However, in both cases these were rare extremes with the majority of all birds moving < 500 m. Therefore, distance moved after release would not have confounded our estimates of survival rates.

Causes of mortality

When dead radio-tagged birds were found, field signs were used to help determine the cause of death wherever possible. Carcasses on roads or shot dead were easily identified, as were those that collided with fences. Where no other cause could be discerned and carcasses were found intact, mortality was recorded as 'disease', although no formal diagnoses were made; these presumably included diseased and starved birds. Where insufficient remains were found to diagnose the cause of death, 'unknown' was recorded. Predation was diagnosed as follows (Thirgood et al. 1998): plucked feathers and 'V'-shaped notches on large bones, and remains found at plucking posts and nests were indicative of raptor predation (nests were not visited directly, but checked via radio-telemetry; it was not possible to distinguish between species of raptor from field signs); red foxes *Vulpes vulpes* left clear signs of chewing on large parts of the carcasses, particularly feathers and radiotags; smaller mammalian predators, such as stoats *Mustela erminea*, rats *Rattus norvegicus* and domestic cats *Felix catus*, left various signs distinct from foxes, like smaller bite marks and eaten patches, and they occasionally moved remains to their burrows. No kills were witnessed directly, but buzzards *Buteo buteo* were seen perched on or near release pens (during most visits to some pens), buzzards and sparrowhawks *Accipiter nisus* were seen attacking live partridges, and buzzards were twice flushed from fresh raptor-killed partridges (carcasses warm, no sign of mammalian predation). No mammalian predators were seen attacking or eating partridges, presumably because they were less conspicuous and most active at night, but stoats occasionally raided, or were caught at, release pens. Uneaten carcasses found buried (i.e. evidence of digging) were assumed to have been predated by red foxes and were often associated with scent marking.

Birds found dead and carcasses found uneaten (N = 18) suggested that scavenging of carcasses was not inevitable within the time between site visits. Two trials were conducted to investigate the rate of scavenging at Kirriemuir. In December 2002, eight woodpigeon *Columba palumbus* carcasses were staked-out at between 10 and 25 m from the edge of fields (cereal stubble, ploughed or winter cereal, therefore offering minimal cover). This was repeated in January 2003 with nine carcasses of red-legged partridges *Alectoris rufa*. Carcasses were assumed to be significantly more conspicuous than average for natural grey partridge deaths, so scavenging during trials should occur significantly quicker, particularly compared to natural deaths occurring in spring and summer when vegetative cover is greater. Carcasses were checked every 1-3 days (mean: 1.6 days) for a total of 14 days.

Four recently dead, unscavenged released birds (three male, one female) were found between December 2002 and February 2003 (fence collisions) and were autopsied by the Scottish Agricultural College Veterinary Science Division to check their body condition and general health.

Breeding rate

The most robust measure of breeding performance available was breeding rate (the proportion of all reared and wild females alive at mid-April that were known to reach at least the incubation stage). Because attempts that failed early (e.g. during egg-laying) would have been less detectable than attempts that lasted longer, breeding rate may have been underestimated.

Hen body condition

All reared and wild hens caught during the early spring were weighed to the nearest 5 g using a Pesola spring balance and their right tarsus was measured to the nearest 0.1 mm using Vernier callipers. Tarsus measurements were taken three times and averaged.

Analyses

Survival and breeding rates were analysed by fitting year and group (e.g. reared or wild hen) as factors, with year*group interactions, within a generalised linear model with binomial error (using the number of birds marked as binomial denominator) and logit link function, with the number of survivors/breeders as the response variable. Tests were based on the likelihood ratio statistic, approximately distributed as chi-square. Differences in the proportion of carcasses assigned to different causes of mortality were analysed using G-tests (with Williams' correction; Fowler et al. 1998). To investigate differences in body condition between tagged reared, untagged reared and wild hens, we used analysis of covariance to test for differences in body weight (logarithms to normalise the data) after adjusting for tarsus length (logarithms) and year, with the year*group interaction. For graphical purposes, we constructed an index of body condition as body weight divided by (tarsus length)^a where a was the coefficient estimated for tarsus length in the latter analysis. All analyses were carried out in GenStat 7.2 (Payne 2004). Interaction terms were not statistically significant and are not reported.

Results

Impact of radiotags

In our experiment, the survival rate of birds carrying a dummy or working radiotag compared to those that did not from release (September) until the night-time surveys in spring (February-early April) was not significantly different ($\chi^2_1 = 2.1$, NS; Table 1), although there were between-year differences ($\chi^2_3 = 3.0$, $P < 0.05$).

Survival rates

The over-winter (September-April) survival rates of birds with visible marks and radiotags were not significantly different (11 ± 2 (SE) and 10 ± 2%, respectively; $\chi^2_1 = 1.6$, NS; see Table 1), but again there were differences between years ($\chi^2_6 = 5.9$, $P < 0.001$). When only including data from the four years where both estimates were available, the survival rates become 13 ± 2 and 21 ± 5%, respectively ($\chi^2_1 = 1.6$, NS).

The survival rate of radio-tagged captive-reared females caught during night-time surveys in spring (February-early April) through to September was 30 ± 8%, which was almost a third less than that (44 ± 8%) for wild females (see Table 1). However, the difference was not statistically significant

Table 1. Impact of radiotags and survival rate estimates. 'Year' refers to year of release in all cases except for 'reared-' and 'wild females', when it refers to the spring/summer in which survival rates were estimated. From 2000 to 2003, dummy tags were fitted to some released birds along with working radiotags as part of an experiment comparing survival rates of tagged and untagged birds (those fitted only with collars). 'Radio-tagged' birds were fitted with working tags (number excludes battery failures and disappeared birds). 'Collared' birds were those carrying just the fabric collar. Data were for both sexes unless stated otherwise. Up to autumn 2000-summer 2001, data were from Arbroath; thereafter from Kirriemuir.

	Number at time t					Number at time t+1					
Year	Dummy & working radiotags	Radio-tagged	Collared	Reared females	Wild females	Dummy & working radiotags[1]	Untagged[2]	Radio-tagged[3]	Collared[4]	Reared females[5]	Wild females[5]
1997		104	-	-	-			3 (3%)	-	-	-
1998		-	78	2	8			-	7 (9%)	0	4 (50%)
1999		-	80	-	-			-	3 (4%)	-	-
2000	39	12	40	2	9	6 (15%)	3 (8%)	1 (10%)	9 (11%)	0	4 (44%)
2001	28	23	32	5	8	8 (29%)	7 (22%)	8 (35%)	15 (25%)	2 (40%)	4 (50%)
2002	22	18	38	15	4	3 (14%)	1 (3%)	2 (11%)	4 (7%)	6 (40%)	2 (50%)
2003	22	13	37	4	3	2 (9%)	4 (11%)	3 (23%)	6 (10%)	1 (25%)	1 (33%)
2004				5	4					1 (20%)	1 (25%)
Totals	111	170	305	33	36	19	15	17	44	10	16
Mean % ± SE						17 ± 9%	10 ± 8%	10 ± 2%	11 ± 2%	30 ± 8%	44 ± 8%

[1] Percentage survival rates between autumn and spring calculated from resightings of birds during spring night-time searches only, carrying dummy and working radiotags. Analyses compared survival rates with those of 'Untagged' birds.
[2] Estimates of survival between autumn and spring for birds with collars only, seen during night-time searches only. See point [1] above also.
[3] Estimates of survival between autumn and spring for radio-tagged birds only, from all radio-locations up to mid-April. Analyses compared survival rates with those of 'Collared' birds.
[4] Percentage survival rates between autumn and spring calculated from resightings only, of all birds up to mid-April. This will have included tagged birds, but it was not always possible to positively identify them during spring surveys. See point [3] above also.
[5] Survival rates between February/April and September for radio-tagged hens.

(χ^2_1 = 1.9, NS) and there was no effect of year (χ^2_5 = 0.5, NS).

Causes of mortality

During the scavenging trials, seven of the eight pigeons and all nine of the partridges were eaten by the end of 14 days. In the first trial, the first carcass was scavenged after three days, whilst in the second, it was eaten on the first day. The average period elapsing before scavenging occurred was eight and five days, respectively. This period of time was longer than that between most site visits (maximum of five days), despite carcasses being relatively exposed. Given this, plus the discovery of uneaten carcasses (N = 18) during radio-tracking and our observations of raptors (see above), we assume in what follows that radio-tagged birds were killed by the predators identified from field signs rather than scavenged.

The most significant cause of mortality for reared birds was predation (82% of losses at Arbroath and 55% at Kirriemuir; Table 2), with red foxes and raptors responsible for the majority of kills. Reared partridges were more likely to be predated than wild birds at Arbroath (G_{1adj} = 5.8, $P < 0.05$), whilst the probability of predation was the same for both groups at Kirriemuir (G_{1adj} = 0.4, NS). Foxes were the prime predator of reared birds at Arbroath, whilst they were second to raptors at Kirriemuir where more rigorous measures to reduce

Table 2. Causes of mortality for radio-tagged male and female captive-reared (N tagged = 203) and female wild (N = 36) grey partridges.

		Number found dead (% of total dead)								
		Predation								
Study site		Raptor	Fox	Other mammal	Disease	Unknown	Road	Shot	Fence	Total dead
Arbroath (4 years)	Reared	7 (14%)	27 (55%)	6 (12%)	2 (4%)	7 (14%)	-	-	-	49
	Wild	3 (19%)	3 (19%)	2 (13%)	4 (25%)	4 (25%)	-	-	-	16
Kirriemuir (3 years)	Reared	22 (34%)	7 (11%)	6 (9%)	12 (19%)	8 (13%)	4 (6%)	3 (5%)	2 (3%)	64
	Wild	5 (56%)	-	1 (11%)	-	2 (22%)	-	1 (11%)	-	9
	Total	37	37	15	18	21	4	4	2	138

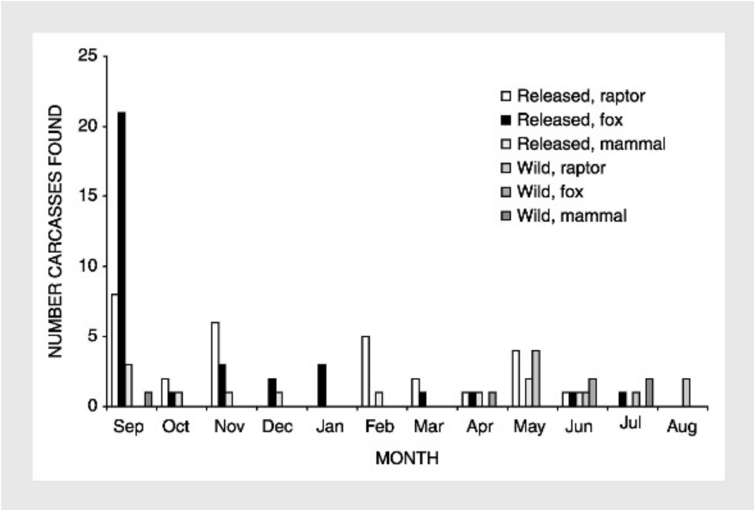

Figure 1. Number of grey partridges predated throughout the year in relation to type of predator. 'Released' are released captive-reared males and females, and 'wild' are wild females only.

the numbers of mammalian predators were undertaken. For wild birds at Kirriemuir, 56% of deaths were due to raptors, but at Arbroath 'disease' was also an important cause of death (25%). The difference in predation rate between the sites was significant for reared birds (G_{1adj} = 9.4, P < 0.01), but not for wild birds (G_{1adj} = 0.7, NS).

The released birds were vulnerable to predation immediately after leaving the pen, with many taken within the first month (Fig. 1). However, predation was also an important cause of mortality throughout the year. Raptor predation occurred throughout the spring and summer months despite the fact that cover from crops and other vegetation was at its greatest.

Breeding rate

Wild females alive in mid-April were three times more likely to try to breed than captive-reared females (χ^2_1 = 14.6, P < 0.01; Table 3). Year had no effect on breeding rate (χ^2_5 = 1.1, NS). If they survived, captive-reared females were able to raise chicks; a female released at Kirriemuir in 2001 fledged 14 young in 2003 before being killed by a buzzard in October. Only two other hens survived into their second year; one was killed by a raptor in February and one died of unknown causes in April. Reared females in their first breeding season were not seen with fledged chicks, although one successfully hatched a clutch of eggs. So of 520 partridges released (around 260 of which were presumably females), one successfully reared young (0.4%), corresponding to 2.8% of females alive at mid-April.

Table 3. Proportion of all captive-reared and wild female grey partridges alive at mid-April that then reached incubation or beyond. Up to 2001 data were from Arbroath; thereafter from Kirriemuir.

	Captive-reared		Wild	
Year	No. survived	No. bred	No. survived	No. bred
1998	1	0	7	5 (71%)
2000	2	0	7	6 (86%)
2001	3	2 (67%)	10	5 (50%)
2002	12	2 (17%)	4	3 (75%)
2003	4	1 (25%)	3	1 (33%)
2004	5	0	4	1 (25%)
Total	27	5	35	21
(% ± SE)		(19 ± 7%)		(60 ± 8%)

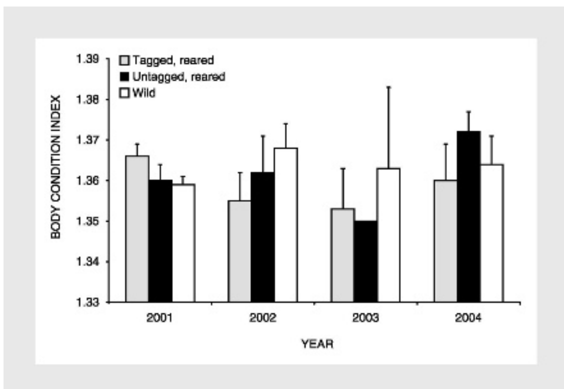

Figure 2. Mean (+ SE) body condition index (see Methods) of radio-tagged reared, untagged reared and wild female grey partridges sampled during the early springs of 2001-2004.

Hen body condition

There was no detectable difference in the body condition of tagged and reared, untagged and reared and wild hens ($F_{2,51}$ = 0.04, NS; Fig. 2). Year also had no effect ($F_{3,51}$ = 0.8, NS).

The autopsies on the four birds killed in collisions with fences revealed that all four were in good health, with normal fat and muscle condition, no endoparasites detected or significant bacteriological findings. All were salmonella negative.

Discussion

Impact of radiotags

Our experiment revealed no differences in the survival rate and body condition of tagged and untagged released partridges, suggesting that this information from tagged birds should reflect that of the population of released birds in general, and that the methods employed here should provide an adequate means of monitoring similar grey partridge release schemes. Caution is needed, however, as the number of survivors in each year was low, so the power to detect significant differences in survival rates and body condition would also be low. However, in three of the four years, and on average, the survival rate for tagged birds was higher than that for untagged birds. This is the opposite of what would be expected if a tag effect were present.

Survival rates

Over-winter survival of radio-tagged reared birds was low (mean 10%), as was the survival rate of radio-tagged reared females during the summer (30%); the only period during which comparisons could be drawn with wild birds (44%). Although the two estimates were not statistically different, the power of the test was low owing to small sample sizes, and it is likely that the difference was genuine. The few studies reporting survival rates of reared grey partridges after release found comparable low rates: in Poland, Panek (1988) reported winter (October-January) survival rates of ringed/wing-tagged captive-reared birds of 12%, and between March and April (i.e. birds released in March) of just 2%. Dowell (1990a) found the survival rate of radio-tagged captive-reared birds in southern England up to 25 days after release was 39-47%. In Finland, Putaala et al. (2001) found that survival rates of radio-tagged birds released in autumn (October-November) and monitored through to January-February were 7-42%, and for spring released birds (March-April) through to August they were just 3%. In Italy, Meriggi et al. (2002) reported survival rates for radio-tagged birds of 19% during the spring and summer, but these birds were offspring of birds released previously that were at least one year old, so they are not directly comparable to the survival rates found in our study.

Other commercially-reared gamebirds also have low survival rates once released (pheasant: Robertson 1988, Millán et al. 2002; red-legged partridge *Alectoris rufa*: Millán et al. 2003), which are usually lower than their wild congeners (grey partridge: Dowell 1990a, Putaala et al. 2001; pheasant: Kraus et al. 1987, Leif 1994). It is not always clear, however, why this should be. Predation is usually the most important proximate cause of death (grey partridge: Panek 1988, Putaala et al. 2001, Meriggi et al. 2002; pheasant: Kraus et al. 1987, Robertson 1988, Brittas et al. 1992, Leif 1994, Millán et al. 2002; red-legged partridge: Millán et al. 2003), but this could be for a number of reasons. Holding large numbers of birds in pens may attract predators and increase predation risk for released birds (Robertson 1988, Dowell 1992). Reared birds may acquire more infections because of ease of transmission between penned individuals, or increased susceptibility to diseases due to higher stress levels. And some studies have shown that the risk of predation in gamebirds is greater for individuals with higher parasite burdens (Hudson 1992, Millán et al. 2002). Also, the use of medication in reared stocks may leave birds immunologically naïve and vulnerable when challenged by pathogens in the wild (Dowell 1992). Birds reared in captivity may also lack the behavioural instincts or experience to recognise or respond appropriately to predators or the threat of predation once released (Dowell 1990a, 1992), which may be directly related to the number of generations reared in captivity (McPhee 2003). Furthermore, birds reared commercially are usually fed on a high-protein, low-fibre diet, which can leave them unprepared for the high-fibre diet available in the wild (Putaala & Hissa 1995, Millán et al. 2003). In most situations more than one factor probably facilitates low survival rates (Dowell 1992). In our study, the reared birds received no medication before release, they had good body-condition indices in spring, the carcasses autopsied were healthy and the proportion of radio-tagged birds lost to 'disease' was low. Therefore, we suspect that their low survival rate may have resulted from increased vulnerability to predation via a combination of increased predation risk at release pens (see Methods) and inappropriate behaviour, although further study is required to confirm this.

Some variation in survival rates was found among years, but it is not clear why. We had no indication of varying quality of the reared birds. Release pens were occasionally moved between years, and the effort invested in legal predator control sometimes varied, as did its effectiveness. Weather conditions were not drastically different among the years.

Causes of mortality

There were differences in predation between sites, with reared birds more likely to be predated at Arbroath than at Kirriemuir, and with mammalian predators (particularly foxes) being most significant at Arbroath, and raptors most significant at Kirriemuir. This was probably due to the more intensive level of legal predator control at Kirriemuir, which seemed to reduce the number of some mammalian predators; fewer foxes were seen at Kirriemuir during night-time surveys in the spring (D.M.B. Parish, pers. obs.). It is also possible that raptors were more abundant at Kirriemuir than at Arbroath, although we have no data on this and they were certainly frequently seen at both sites. It is interesting to note that the presence of the gamekeeper at Kirriemuir did not reduce the rate of predation on wild birds relative to that at Arbroath despite reducing losses to mammalian predators, as they then mostly fell prey to legally protected raptors. Raptor predation rates have not been reported for wild grey partridge in the UK before, but our estimates (19-56%) are comparable to those reported elsewhere; Carroll (1990) attributed 47% of deaths to raptors in North Dakota between January and April (100 birds radio-tagged), whilst Bro et al. (2001) found 29% of losses due to raptors in France between March and September (1,009 birds tagged).

Partridges are probably more vulnerable to raptor predation on farmland today because of lack of vegetative cover (Reitz & Mayot 1999), particularly during the winter and because sparrowhawks (Gibbons et al. 1993, Baillie et al. 2005) and buzzards (Baillie et al. 2005) are more common now than decades ago. Raptors took partridges throughout the year, including the spring and summer, when cover from vegetation was greatest. This strengthens our assertion that these predators are mostly killing partridges and not scavenging them, as most carcasses would presumably be difficult to spot at this time of the year.

Breeding rate

Reared hens attempted to breed at a significantly lower rate than wild hens. Other measures of breeding success were not considered because of the small numbers of hens surviving the breeding season. Poor breeding success of released gamebirds relative to their wild congeners in their first summer is typical (Hill & Robertson 1988, Brittas et al. 1992, Leif 1994), but poor breeding success is also typical of young birds generally (e.g. Newton 1989, Sæther 1990). Increasing the proportion of released partridges surviving into the second year could have a big impact on productivity and therefore on the success of reintroduction schemes.

Hen body condition

The body condition of captive-reared female partridges was similar to that of wild females during early spring. Few birds died of 'disease' (sick and malnourished birds), and autopsies on the four released birds killed in collision with wire fences revealed that they were in good health. This is important, as it suggests that the reared birds did not struggle to find sufficient food to maintain a healthy body condition over winter. This contrasts with the situation found in pheasants where released birds generally have poorer body condition than wild birds (Draycott et al. 2002) and require supplementary feeding to maintain good body-condition indices (Draycott et al. 1998). Body condition has been found to influence productivity in released pheasants (Draycott et al. 1998), and if the same is true of partridges, successful breeding of released females in our study would not have been hampered by poor body condition.

Commercially-reared grey partridges should not be used in reintroduction programmes unless their survival rates could be improved. We found pre-breeding hens to be in good condition and the one hen that survived into her second breeding season bred successfully. Released birds in our study were clearly vulnerable to predation, and legal predator control would be a prerequisite to any release. Release sites away from raptor habitats would also be important where raptors are common. Other measures should also be established before releasing partridges, such as the provision of insect-rich habitats during the summer (Sotherton 1991) and of nesting cover (Potts 1986, Rands 1986).

In addition to increased predation risk at the release pen, reared partridges may have been vulnerable to predation owing to inappropriate behaviour (Dowell 1990a), and methods of overcoming this should be investigated. Released birds might learn to recognise local predators and the appropriate behavioural responses from wild birds where these are present. Otherwise, it has been suggested that it is possible to teach naïve individuals the appropriate anti-predator behaviour where the species has not evolved in isolation from predators (Griffin et al. 2000), as is the case for the grey partridge. Indeed, grey partridges have a number of genetically determined, anti-predator behaviours (Dowell 1990b). It is not yet clear how best to train captive-reared birds, but where possible it should involve wild birds that can be identified as an appropriate model (Griffin et al. 2000, J. Heatley, unpubl. data).

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