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Breeding dispersal and demography of wild and hand-reared grey partridges *Perdix perdix* in Finland

Ahti Putaala & Raimo Hissa

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To evaluate the usefulness of restocking of grey partridge *Perdix perdix* in marginal ranges we studied survival, spring dispersal and breeding success of wild and released grey partridge females using radio-tracking. Released females had lower survival during the breeding period than wild females. Within the limitation of the small sample size obtained from the released birds surviving till nesting, there was no difference in spring dispersal, nesting chronology, clutch size, and nest predation between wild and released birds. However, wild partridges produced more fledglings per radio-tracked female than released birds. This difference was mainly due to the higher survival rates of wild hens compared to those of released hens before the incubation period. We conclude that due to their poor survival and reproduction output, released birds may have little value in attempts to boost threatened wild populations of the grey partridge, whereas habitat management and predator control could be more useful tools for the preservation of grey partridge populations in marginal regions.

Key words: breeding, clutch size, grey partridge, hand-rearing, Perdix perdix, survival, restocking

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A marked decrease in the number of grey partridges *Perdix perdix* has been noticed over the entire holarctic distribution area since the 1950s (Potts 1986). Along with the decrease in numbers, the distribution area of the grey partridge has contracted and become more patchy. The ultimate reason for this threatening trend is modernisation of agriculture (Potts 1980, 1986; Birkan, Serre, Pelard & Skibniewski 1990), although the demographic key factors regulating population levels vary at different sites within the distribution area of the grey partridge (see Potts 1986, Carroll 1990, Panek 1992). To increase natural populations, releases of hand-reared birds have become common in recent decades. Supplementing birds available for shooting is still a strong motive for releases within the core range of the distribution area of grey partridges, but conservational aims take precedence in releases conducted in marginal regions. The main purpose of the releases in marginal areas is to increase the size of the breeding population. However, little research has been conducted to compare the breeding demography of wild and released birds. The aim of this study was to evaluate demographic breeding parameters of wild and released grey partridges in a marginal region of their distribution area. The present study is part of a research project examining the effects of captive-rearing on physiology, behaviour and viability in gallinaceous birds

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which is conducted by staff of the Department of Biology.

Methods

We conducted this study on a research area of 20 km^2 in the centre of mixed arable land in the municipality of Tyrnävä (64°46'N, 25°40'E), central Finland. The crops grown in the study area include spring barley and oat (50-55% of the arable land in the area); pastures and grass hayfields (20%), fallows and idle fields (10-20%) and potato fields (5-10%) are also present. Farmsteads and forest stands make up ca 6% of the study area. The field size in the study area averages 4.4 ha. The wild partridge population in the study area is the most northerly in the distribution range of the species. Winter densities of the population varied between 3.2 and 7.0 individuals/km^2 during the study years.

Wild grey partridges were caught using walk-in traps on winter feeding places. Birds were weighed, marked with numbered metal rings and fitted with radio-transmitters. To study survival and productivity of hand-reared birds in the wild, a total of 48 hand-reared hens fitted with radio-transmitters were released in the study area between late March and early April in 1991 (18), 1992 (10) and 1996 (20).

Two kinds of radio-tags, a necklace type (9 g, TW-2, Biotrack, UK) or a backpack transmitter (15 g with a harness, SR-1, Biotrack, UK) were used to track wild and released partridges in 1991. Necklaces (N) and backpacks (B) were used in equal proportions on wild (6 N and 6 B) and released (9 N and 9 B) grey partridges. In subsequent years, only one type of transmitter (backpacks in 1992-95, necklaces in 1996) was used for both groups.

A portable receiver (CE-12, Custom Electronics of Urbana, Illinois) and a hand-held, five-element Yagi antenna was used for radio-tracking. An aircraft (Cessna 172) was used once or twice each spring in the search for dispersing radio-tagged partridges. We determined spring dispersal of wild partridges as the distance between the capture site and the first nest site of each hen. In the case of released partridges, we measured the dispersal distance between the release site and the first nest site of each hen.

Each bird was located 2-3 times per week before the onset of incubation. Incubating hens were controlled by triangulation from near distance at least every other day. If the hen was located off the nest, the nest was checked for possible failure or hatching. Otherwise the nest was first checked and eggs were counted in the second week after the beginning of incubation, when the risk of nest abandonment was reduced (Potts 1986). Nest location and vegetation concealment in a 0.5 m × 0.5 m square, with the nest situated in the centre of the square, were recorded. The degree of nest concealment was visually estimated from a distance of 2 m from the incubating hen. A four-stage scale was used in the definition of concealment: 1) excellent: hen totally concealed; 2) good: hen partly visible; 3) fair: hen mostly visible; 4) poor: hen totally visible. The nest was finally examined after hatching, and the number of hatched and unhatched eggs was counted. We calculated the clutch initiation date regressively from the onset of incubation assuming a laying rate of 1.1 days per egg (McCabe & Hawkins 1946). We calculated initiation of incubation by backdating (25 days) from the hatching date. Radio-tracked broods were flushed four weeks after hatching to determine chick survival. Although grey partridge males also take part in the brooding of chicks, we considered all chicks in a brood lost if the hen died within three weeks after hatching, up to which age chicks depend on the occasional brooding by parents (Marjoniemi, Hohtola, Putaala & Hissa 1995).

We calculated survival probabilities for radio-tagged birds using the Kaplan-Meier procedure (Kaplan & Meier 1958) and used a log-rank test to assess differences in survival between wild and released females. We used Student's t-test with log-transformed numbers to compare dispersal distances, and Mann-Whitney U-test to compare nesting parameters between wild and released birds. We compared the proportion of successful nests between the two groups using Fisher's Exact test, and the hatchability of eggs using χ^2-test. The relatively small size of nest data impeded statistical analyses of potential year and age-specific differences in breeding parameters.

Results

From the population of radio-tracked birds, two wild and four released hens disappeared before clutch initiation had been documented and they were excluded from further dispersal and nesting analyses. Break up of coveys and pair formation among wild birds in the study area took place in early April. The released

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females were also accompanied by wild males within two weeks after the release. Movements associated with pair formation and searching for a suitable nesting habitat usually lasted 3-4 weeks after which pairs settled down and restricted their movements to within the pair home-range.

In total, 33 nests of wild partridges and eight nests of released partridges were found during the study period. The data on wild nests comprised 27 nests of radio-tagged females and another six nests found via radio-tagged males, who stayed near the nests during incubation. We considered three late nests (initiated after 1 June) of wild hens as renests, and excluded them from the statistical analyses. All nests identified as nests of released hens were first nests. Annual numbers of grey partridges radio-tracked, first nests found, broods hatched and fledglings recruited, are given in Table 1.

Survival of hens

Kaplan-Meier estimate of spring survival probability (from the beginning of April to the median date of the onset of incubation) of radio-tagged wild hens was significantly higher ($\chi^2_1 = 30.54$, $P < 0.001$) than the survival probability of released hens during the same period (Table 2). However, there was no difference in survival probability between wild and released females once the incubation had started ($\chi^2_1 = 1.39$, $P = 0.24$). Due to their higher initial mortality rate, the survival probability of released females (0.04 ± 0.03, x ± SE) during the breeding season (from early April to the end of August) was lower ($\chi^2_1 = 30.35$, $P < 0.001$) than that of the wild females (0.30 ± 0.07) (Fig. 1). Predation was the main cause of mortality in both wild and released birds. More detailed information about mortality factors of grey partridges in Finland will be given in Putaala, Turtola & Hissa in press.

Table 1. Annual numbers of wild and released radio-tracked females, first nests found, broods hatched and fledglings surviving to the age of four weeks in Tyrnävä.

	1991	1992	1994	1995	1996
Females tracked					
Wild	12	1	9	13	7
Released	18	10	0	0	20
First nests found					
Wild	10	0	5	9	6
Released	2	4	0	0	2
Broods hatched					
Wild	6	0	5	7	6
Released	0	3	0	0	2
Broods survived					
Wild	4	0	2	4	3
Released	0	0	0	0	1
Fledglings survived					
Wild	37	0	27	22	22
Released	0	0	0	0	2

Table 2. Values of demographic breeding parameters of wild and released grey partridges in northern Finland, 1991-1996.

	Wild	Released	P
Hen spring survival[1] (N)	0.686 (42)	0.185 (48)	< 0.001
No of nests[2]			
Attempts	30	8	
Succesful (%)	24 (80.0)	5 (62.5)	n.s.
Clutch size			
Mean ± SE (N)	20.54 ± 0.33 (28)	19.25 ± 0.70 (8)	n.s.
Range	17 - 24	17 - 23	
Eggs hatched			
Mean ± SE (N)	18.04 ± 0.70 (23)	18.00 ± 1.10 (5)	n.s.
%	87.9	94.7	n.s.
Brood survival[3]	0.54	0.20	n.s.
Productivity[4]	2.09	0.05	

[1] Survival of wild birds from the beginning of April to median date of incubation, and survival of released birds from the release to median date of incubation
[2] Includes only first nests in which incubation was initiated
[3] Proportion of broods surviving from hatching to the age of four weeks
[4] Fledglings per radio-tagged females alive/released in early April; females disappearing during the study were not included.

Dispersal

The dispersal distance of the 24 wild hens (arithmetic mean = 3,140 ± 525 m (SE), geometric mean = 2,096 m, median = 3,200 m) did not differ significantly ($t_{30} = 0.51$, $P = 0.62$) from the dispersal distance of eight released hens (arithmetic mean = 2,324 ± 764 m, geometric mean = 1,712 m, median = 1,370 m). One deviant value occurred in the dispersal data of

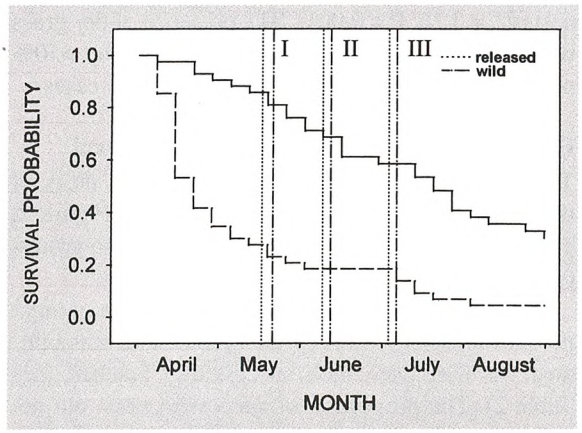


Figure 1. Kapplan-Meier survival estimation curves for radio-tagged wild (—) (N = 42) and released (– –) (N = 48) female grey partridges during April - August. The initiation of egg laying (I), incubation (II) and hatching (III) is expressed as median values.

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both wild and released partridges; one wild hen had moved 10,800 m and one released hen had moved 7,100 m before nest initiation. Correlation analyses performed with wild female data did not show any significant relationship between female winter weight, dispersal distance, nest initiation date and clutch size.

Nesting chronology

The median date of initiation of egg laying was 20 May for wild (N = 26) and 16 May for released partridges (N = 7) (see Fig. 1). Clutch initiation did not differ between the groups (Z = 1.04, P = 0.30). The median date of onset of incubation was 11 June in wild and 8 June in released birds. The median peak date of hatching was 5 July in wild and 2 July in released birds. The timing of incubation and hatching were similar for wild and released partridges (Z = 1.14, P = 0.25, same for incubation and hatching).

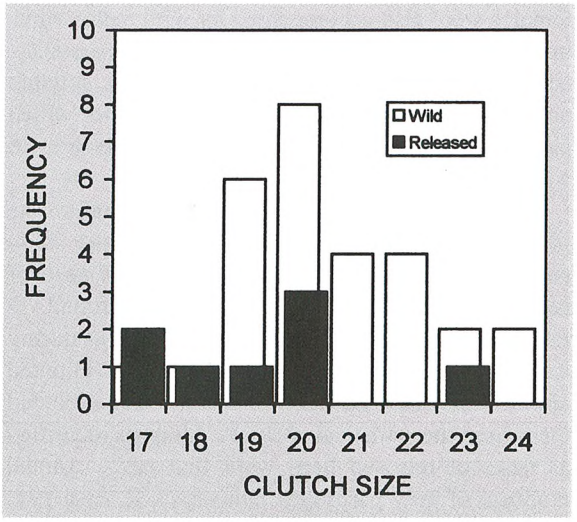


Figure 2. Clutch size distribution of wild and released grey partridges in the study area.

Characteristics of nest site

The distribution of nest sites was similar for wild (N = 30) and released (N = 8) partridges (Z = 0.53, P = 0.60). Partridges' preference for residual linear nesting cover seemed evident as the majority (63%) of the nests were located on ditch banks; the rest of the nests were established either in fallows (32%), along road sides (2.6%) or in hayfields (2.6%).

The degree of nest concealment did not differ between wild and released partridges (Z = 1.13, P = 0.26). In the combined nest data 15 (39.5%) were rated to have excellent, 10 (26.3%) good, 7 (18.4%) fair and 6 (15.8%) poor concealment. Successful nests had a better concealment rate than unsuccessful nests (Z = 3.26, P = 0.001). The presence of dry grass was recorded on all nest sites, and it made up >50% of the concealing vegetation in 21 out of 38 cases.

Clutch size, nest success and chick survival

The distribution of clutch size in the first nests of wild and released females is presented in Figure 2. The clutch size did not differ between the two groups (see Table 2).

In 24 of 30 wild partridge nests and in five of eight nests of released birds in which incubation was initiated, at least one chick successfully hatched (see Table 2). The proportion of successful nests did not differ between the two groups (Fisher's exact test, P = 0.36). Of the six unsuccessful nests of wild hens, predation of a hen at the nest was responsible in three, egg predation in two and desertion in one case. Correspondingly, the reasons for nest failures of released females were hen predation in two cases and egg predation in one case.

The brood production rate for radio-tagged females which successfully hatched chicks was 0.525 for wild and 0.114 for released hens, respectively. The mean number of hatched chicks per successful nest did not differ (Z = 0.11, P = 0.91) between wild and released partridges (see Table 2). In successful nests, the egg hatchability was 87.9% and 94.7% for wild and released birds, respectively, and did not differ between the two groups ($\chi^2_1 = 0.145$, P = 0.70). In the pooled data, hatchability was not related to clutch size (r = -0.065, P = 0.74, N = 28).

Three renests of wild partridges with clutch sizes of 7, 11 and 13 were encountered. Although chicks hatched in two of these nests, no fledglings were recruited from the renests.

Eleven of 24 wild partridge broods and four out of five broods reared by released females were unsuccessful, i.e. recruiting no fledglings. With the exception of two cases where a wild pair lost all their chicks, all other total brood failures resulted from the death of the hen within three weeks after hatching. The mean chick number in the 13 wild broods surviving to the age of four weeks was 8.85 ± 1.49 (SE), and the chick survival in these broods was 0.467. Including unsuccessful broods, the chick survival up to four weeks of age was 0.277 in radio-tracked wild broods (N = 24). Productivity expressed as the number of 4-week-old fledglings per radio-tagged hen

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alive (wild) or released at the beginning of April was much lower in released than in wild birds (see Table 2).

Discussion

Adult survival

The radio-transmitters did not no seem to affect the behaviour or flying ability of partridges. However, our recent study with optoelectronic motion analysis system revealed that radio-transmitters may lower the take-off angle, flight speed and climbing rate of grey partridges (Putaala, Oksa, Rintamäki & Hissa 1997). Reynolds, Dowell, Brockless, Blake & Boatman (1992) also suspected that backpack radio-transmitters may increase scent spreading from the back of incubating grey partridges and, thus, may make them vulnerable to mammalian predators. However, in our study, incubating radio-tagged hens had quite high survival. Therefore, without comparative follow-up research of instrumented and non-instrumented birds during the incubation period, it is difficult to evaluate whether the radio-transmitters used in our study actually affected the survival of the partridges. We feel confident, however, that results from the radio-tracking of wild and released birds are well comparable as both bird groups carried similar transmitters, or different transmitter types in equal proportions at the same time. Furthermore, our data from 1991, when necklace and backpack transmitters were used contemporarily for radio-tagging of female and male grey partridges, did not reveal differences in survival which could be ascribed to the type of transmitter (Putaala & Hissa 1993, Putaala et al. in press). During the breeding period, released grey partridge females had much lower survival rates than wild females. This outcome is in concordance with results obtained in similar comparative studies involving pheasants *Phasianus colchicus*. Hill & Robertson (1988) documented a threefold risk of predation for released pheasant females during the breeding season compared with that of wild females. Lower survival of released female pheasants over the breeding season was also reported by Brittas, Marcström, Kenward & Karlbom (1992) and Leif (1994). Due to the poor survival of released grey partridges, it was difficult to achieve a sample size large enough for comparison of demographic breeding parameters between wild and released birds. Therefore, the results should be interpreted with caution.

Regarding pair formation, spring movement, clutch initiation, egg laying and incubation, the released females seemed to have behavioural patterns similar to those of their wild counterparts. However, the poor survival of released birds indicates deficiencies in their anti-predator behaviour. Behavioural studies with artificial predator models have verified the inadequate anti-predator behaviour of hand-reared partridges (Dowell 1990, Anttila, Putaala & Hissa 1995).

Although no parameters in breeding indicated differences in the physiological condition of released and wild birds, it cannot be totally ruled out that the physiological effects of captive rearing (see Paganin & Meneguz 1992, Putaala & Hissa 1995) may affect the survival of released birds especially within the first weeks following the release, when the mortality of released birds is highest (see Fig. 1, see also Hessler, Tester, Siniff & Nelson 1970, Brittas et al. 1992, Putaala et al. in press).

Spring dispersal

The chronological progress of covey break up and pair formation of wild grey partridges registered in our study followed the description of Birkan & Serre (1988). We did not observe pair isolation, defined by Church, Harris & Stiehl (1980), as a first pattern of behaviour associated with pair dispersal. Otherwise, the two additional behavioural patterns of spring dispersal described by Church et al. (1980), exploration and settlement of pairs, were well recognisable in our study.

The spring movement of Finnish grey partridges bear more resemblance to that of North American rather than that of central European birds. Dispersal distances of radio-tracked females in our study area were similar to those found in Wisconsin, where the maximum spring movements of nine radio-tagged females averaged 2.2 ± 0.4 km (SE) (Church et al. 1980). The spring dispersal distances of grey partridges are much shorter in England (0.42 ± 0.08, Potts 1986) and in France (0.80 ± 0.12, Birkan & Serre 1988) than in Finland.

Potts (1986) suggested that grey partridge pairs in England are spacing themselves out in spring to avoid density-dependent predation. However, the fact that partridges disperse further away at the northern limit of their range despite the much lower density than in the core areas, suggests that density-dependent predation is not the primary reason for long spring movement, at least not in the northern ranges.

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Furthermore, it is not probable that a shortage of nesting cover would induce long movements in northern Finland since enough suitable nesting cover is available for even much higher partridge densities. This is due to small field size and an abundance of permanent linear cover in the field boundaries. Consequently, it is suggested that spring movements of grey partridges at their northern range are primarily motivated by the search for suitable pair and brood habitats. Additional information on the subject will be obtained from the currently ongoing analyses of habitat use of pairs and broods in our research area.

Nesting

Nesting data based on radio-tracking give a reliable picture of nesting chronology, distribution of nest places and nest survival. Data based on systematic searches of nests without radio-tracking can be biased by the subjective impression of potential nest places of a seeker and by the differences in the detectability of nests between habitats. In addition, nests detectable for a human may be easier to find and thus be more vulnerable to predation than a random nest found with the aid of radio-tracking (see Carroll, Crawford & Schulz 1990). Data on nest locations from our study area support the general picture that grey partridges are attracted to permanent linear cover for nesting (Potts 1986, Carroll et al. 1990). Ditch banks were the most important nest places in Finland, whereas in England it was hedgerows (Potts 1986) and in North America roadsides (Carroll et al. 1990, Carroll & Crawford 1991). However, apparently due to shortage of permanent cover, most of the grey partridges' nests in France (Serre, Birkan, Pelard & Skibniewski 1989) and Germany (Kaiser & Storch 1996) are located in winter cereals.

The grey partridge has the largest clutch size of any species of bird. We found the mean clutch size of grey partridges in the population studied to be the highest reported this far. This was predictable since we were dealing with the most northern population of partridges. The mean clutch size of partridges has been shown to follow the general clutch size theory of birds in temperate regions (Cody 1966) increasing with geographical latitude (Lack 1947, Pulliainen 1971). In addition to larger clutch size, the higher chick production of partridges seems to be promoted by higher survival of nests in our study area. While the proportion of successful nests has been documented to vary between 50 and 60% in central Europe (Potts 1986, Olech 1988, Rands 1988) and only 16-40% in North America (Church 1984), over 70% of nests were successful in our study area. High nesting success of both wild and released partridges is probably attributable to high availability of proper nesting cover and low density of nests and therefore low predation pressure on eggs and incubating hens. Although nest survival did not differ between the groups, radio-tagged wild hens had higher brood production rates than released hens attributable to higher survival rates of wild birds.

Reproduction output

Although the fate of the chicks could not be properly confirmed in the cases where a hen died within three weeks after hatching, we considered all the chicks dead despite the fact that the male may have survived and may have been able to take care of the chicks. The calculated figure of 0.277 is thus a minimum value for the chick survival in the radio-tracked wild broods. The chick survival in our study area is a little lower than that found in Sussex, England, where the long-term (1968-1993) chick survival up to the age of six weeks averaged 0.283 (Potts & Aebischer 1995). On the other hand, excluding total brood failures, the chick survival rate in our study area would be 0.467. Thus, it seems clear that the large proportion of unsuccessful broods is the main reason for the low productivity of partridges in the marginal habitat of their northern range in which our study area lies.

The average proportion of unproductive females, i.e. females succeeding in nesting but recruiting no fledglings, was rather high (46%) in Finland in comparison with the corresponding values of 26% in Poland (Chlewski & Panek 1988) or 37% in France (Reitz 1992). The main reason for the large proportion of unproductive females in our study area was not nest failure, but high mortality of hens with brood. Six of the nine hens that died during the brooding period were killed by domestic or feral cats *Felis catus*, which, therefore, significantly decreased the reproduction rate of the partridges in the study area. Conclusions based on the nesting data collected via radio-tagged birds suggest that population dynamics of grey partridges in the marginal range studied is regulated more by brood rather than chick survival rate *per se*. The high proportion of unsuccessful broods in the population studied is at least partly compensated for by a very high clutch size and high nest survival.

Because released females initiated nesting at the same time, produced similar clutch sizes and hatched

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as many eggs as wild females, it seems probable that the physiological condition of released females during breeding did not differ from that of wild females. Perhaps the released birds had enough time to adapt themselves to living in the wild before the breeding period started. However, one difference was apparent in the lower productivity of released females. This is in agreement with the observation of Rands & Hayward (1987), who also documented lower recruitment of fledglings of released partridges than of wild birds. On the other hand, Rands & Hayward (1987) reported similar survival rates for released and wild birds and concluded that poorer productivity of released partridges may have been a result of higher nest failure connected with poorer nest site selection. However, they did not give any data to support that conclusion. In our study, no supporting evidence for the poorer nest concealment or higher nest failure rate of released birds was found. The lower productivity of released partridges than of wild birds due to the higher mortality of released birds is in agreement with the results obtained from similar studies with pheasants (Hill & Robertson 1988, Brittas et al. 1992, Leif 1994).

Robertson (1991) suggested that wide-scale releases of hand-reared birds have decreased brood production rates of pheasants in England, because a large proportion of the breeding birds is annually composed of poorly breeding released birds. Theoretically, massive releases of hand-reared birds can have a negative rather than a positive impact on reproduction output of the recipient population in several ways. First, released birds compete with their wild counterparts for optimum habitats with adequate food supplies, cover and nesting places. The productivity potential of the best breeding habitats may be underexploited if occupied by released birds. Secondly, released birds increase population density, which may lead to greater density-dependent nest failures (Potts 1986). Thirdly, especially with monogamous birds, release of hand-reared birds may prevent effective breeding by wild birds because these mate with released birds having low reproduction rates. Moreover, long-term captive breeding presumably lead to adaptional changes in the genetics of the reared animals. Individuals exhibiting the highest tractability and tameness in captivity will most likely pass their genes to the next generation. Genetic deterioration of recipient, small wild population in large-scale releases is thus a potential risk which should be taken into account. Finally, hand-reared birds may introduce diseases and parasites to wild stock (Viggers, Lindenmayer & Spratt 1993) which can reduce the reproductive output of the birds (Hudson 1986, Woodburn 1995). Further research dealing with the effects of releases on wild populations is still urgently needed before such practice can be routinely employed.

Predation, as shown in a recent study conducted in England (Tapper, Potts & Brockless 1996), may well keep the number of wild partridges below the carrying capacity of the habitat. The substantial effect of predation on breeding numbers of grey partridges was also confirmed in our study. Therefore, our recommendations for the management of the grey partridge are to invest in habitat management for the extant wild population and in predator control instead of relying on releases of hand-reared birds including high economical expenses and risks for the recipient wild populations.

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