Impact of radio-tracking on black grouse *Tetrao tetrix* reproductive success in the French Alps

Alain Caizergues & Laurence N. Ellison

Caizergues, A. & Ellison, L.N. 1998: Impact of radio-tracking on black grouse *Tetrao tetrix* reproductive success in the French Alps. - Wildl. Biol. 4: 205-212.

From 1991 to 1995, we tested the effects of radio-tracking, including trapping, handling and monitoring, on reproductive success of black grouse *Tetrao tetrix* hens in the southern French Alps. Reproductive success (total young/total hens with and without broods) was lower in hens marked with radio-collars than in unmarked hens (0.77 vs 1.66 young/hen, P = 0.02). Brood size was similar in the two groups of hens, but the proportion of hens rearing a brood was lower among marked hens (23 vs 45%, P = 0.03). Reproductive success of hens marked at the beginning of laying, or just before, was lower than that of hens marked ≥6 months before laying (0.25 vs 1.20 young/hen, P = 0.058). The success of hens marked near the time of laying was also low compared with unmarked hens in all years but 1992 (the year*time of capture interaction was significant). In contrast, reproductive success of hens marked ≥6 months before laying was not statistically different from that of unmarked hens (1.20 vs 1.66 young/hen, P = 0.28). Higher predation rates on first clutches, and to a lesser extent lower ability to renest, were responsible for the lower reproductive success of hens marked at the beginning of or just before laying. Altogether, these results suggest that initial discomfort caused by the transmitter, stress of capture, handling and monitoring following capture may temporarily alter the behaviour of hens, thereby increasing detection of their nests by predators. After a period of adjustment, radio-transmitters *per se* may have little or no adverse effect on reproduction. We conclude that to obtain reliable estimates of breeding parameters of black grouse in the French Alps using necklace type transmitters, hens must be equipped with these several months before laying, and nesting hens should not be approached closer than 20 m during radio-tracking.

Key words: black grouse, effect of time of capture, French Alps, necklace radio-transmitters, radio-telemetry, reproduction, Tetrao tetrix

Alain Caizergues & Laurence N. Ellison, Office National de la Chasse (ONC), Direction de la Recherche et du Développement, C.N.E.R.A. Faune de montagne, 8, impasse Champ Fila, F-38320 Eybens, France*

**Present address: CEFE/CNRS, 1919 Route de Mende, F-34293 Montpellier Cedex 5, France - e-mail: keke@cefe.cnrs-mop.FR*

Received 19 May 1997, accepted 16 June 1998

Associate Editor: Kjell-Einar Erikstad

Marking individuals is often a necessary step in detailed studies of demography or behaviour. A critical assumption is that marking has no adverse effects and therefore provides reliable estimates of the variables being studied. Although this assumption may be met in many cases, virtually all marking methods alter the behaviour of individuals to some extent, and thus potentially bias the estimation of demographic parameters, behaviour, metabolic rate, locomotion, and habitat selection (White & Garrot 1990, Calvo & Furness 1992).

Radio-tracking is frequently used on gamebirds because data are difficult to collect using other methods. Because radio-transmitters are heavier and more cumbersome than most other marking methods, they may have greater effects on behaviour, reproduction and survival than e.g. rings or wing-tags. Negative effects of radio-transmitters have been documented in galliforms (McEwen & Brown 1966, Boag 1972, Lance & Watson 1977, Erikstad 1979, Herzog 1979, Johnson & Berner 1979, Warner & Etter 1983, Marks & Marks 1987), anatids (Greenwood & Sargeant 1973, Gilmer, Ball, Cowardin & Reichmann 1974) and in the American woodcock *Philohela minor* (Ramakka 1972, Horton & Causey 1984). In some cases, radio-tracking caused substantial changes in behaviour, survival or reproduction, depending upon species or population (Lance & Watson 1978, White & Garrot 1990), gender or quality of individuals (Lance & Watson 1978, Johnson & Berner 1980), transmitter weight (Warner & Etter 1983) and method of attachment (Small & Rusch 1985, Marcström, Kenward, & Karlbom 1989, Houston & Greenwood 1993, Rotella, Howerter, Sankowski & Devries 1993, Paquette, Devries, Emery, Howerter, Joynt & Sankowski 1997).

A short review of the literature on gallinaceous birds (summarised in Table 1) shows that the method of attachment is important. Radio-transmitters mounted on harnesses or ponchos have been shown in some studies to alter behaviour, reproduction and/or survival, whereas those mounted as a necklace are less cumbersome and less conspicuous and have minimal or no effects (see Table 1 and references therein). However, because most of these studies either compared different methods of attachment or radio-marked vs ringed and/or disturbed individuals (see Table 1), it would be imprudent to consider necklace transmitters innocuous. In other words, even though radio-transmitters *per se* may not constitute a great handicap, trapping along with handling and monitoring may alter the behaviour of the bird to some extent, thereby decreasing, at least temporarily, its reproductive ability and/or survival (Calvo & Furness 1992).

Furthermore, because of the short life expectancy of radio-transmitters (usually less than one year) the duration of the possible negative effects of radio-tracking has rarely been investigated. For these reasons, many authors have urged further studies of the

Table 1. Effects of radio-tracking upon survival, reproduction and behaviour in gallinaceous birds according to the method of attachment (-: negative effect, 0-: minimal effect, 0: no effect, x: not investigated). Notice that all of these studies compared either two methods of attachment or radio-marked vs ringed/back-tabbed individuals and that many did not use control groups.

Species	Method of attachment	Control	Survival	Reproduction	Behaviour	Condition	Author(s)
Blue grouse	Harness	Ringed	0	0	0	Wild	Hines & Zwickel (1985)
Spruce grouse	Harness	Ringed	0-	x	0	Wild	Herzog (1979)
Sharp-tailed grouse	Poncho	Ringed	-	x	x	Wild	Marks & Marks (1987)
Red grouse	Harness	Ringed	x	x	-	Captive	Boag (1972)
Red grouse	Harness	Back-tabbed	0	0	0	Wild	Boag et al. (1973)
Red grouse	Harness	Back-tabbed	x	0-	0-	Wild	Lance & Watson (1977)
Ruffed grouse	Harness	Poncho	-	x	0	Wild	Small & Rusch (1988)
Willow grouse	Harness	Ringed	x	-	-	Wild	Erikstad (1979)
Ring-necked pheasant	Harness	None	-	x	x	Wild(released)	Johnson & Berner (1980)
Ring-necked pheasant	Harness	None	-	-	x	Wild	Warner & Etter (1983)
Wild turkey	Harness	None	x	x	0	Captive	Nenno & William (1979)
Blue grouse	Poncho	Ringed	-	x	-	Wild	Pekins (1988)
Lesser prairie chicken	Poncho	None	-	x	x	Wild	Burger et al. (1991)
Ring-necked pheasant	Harness	Ringed	-	x	x	Wild	Marcström et al. (1989)
Ring-necked pheasant	Necklace	Ringed	0	x	x	Wild	Marcström et al. (1989)
Black grouse	Necklace	Ringed	0	x	x	Wild	Willebrand (1988)
Rock ptarmigan	Necklace	Ringed	0	x	x	Wild	Cotter & Gratto (1995)
Rock ptarmigan	Harness	Ringed	-	x	x	Wild	Cotter & Gratto (1995)
Red grouse	Necklace	Ringed	0	0	x	Wild	Thirgood et al. (1995)

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

effects of radio-tracking (e.g. Lance & Watson 1977, White & Garrott 1990, Calvo & Furness 1992).

Therefore, we compared reproductive success of radio-marked and unmarked black grouse *Tetrao tetrix* hens in the wild. We also investigated, among radio-marked hens, the effect of time of capture on reproductive parameters. This allowed us to separate temporary from permanent effects of radio-tracking.

Methods

The study was conducted from 1991 to 1995 in the southern French Alps at Ristolas (44°47'N, 6°57'E; Queyras, department of the Hautes-Alpes).

Black grouse occur in a subalpine forest (1,700-2,400 m a.s.l.) dominated by larch *Larix decidua*, arolla pine *Pinus cembra*, and mountain pine *P. uncinata*. Ground vegetation consisted mainly of bilberries *Vaccinium myrtillus*, alpenrose *Rhododendron ferrugineum*, and grasses *Calamagrostis* spp., *Festuca* spp.

Average annual precipitation is 833 mm, with peaks of rainfall in June and November (Ascensio 1983). July and August are relatively dry. Average snow depth from January to March varies from 1.3 to 2.0 m. Mean minimum temperature from January to March is -4°C (mean maximum = +3°C) and in July and August the mean minimum temperature is +8°C (mean maximum = +19°C).

Female black grouse were captured using drop-nets on leks during spring display and lily-pad traps in spring, summer and fall (Liscinsky & Bailey 1955). Furthermore, pointing dogs were used to locate broods and the young were flushed into nets. Birds were classified as juveniles (2-10 months), yearlings (10-22 months) or adults (>22 months) on the basis of primary feather pigmentation (Helminen 1963). Some hens had probably initiated laying at the time of capture, but none had started incubating. Some females captured in summer were only seven weeks of age when equipped with radio-transmitters.

Birds were fitted with necklace radio-transmitters with an expected lifespan of 1-2 years. Transmitters weighed 10-15 g for juveniles and 15-17 g for yearlings and adults, i.e. ~2% of the body mass of females at the time of capture.

Females were located at least once a week using a portable receiver and a hand-held yagi antenna. To reduce disturbance, we tried to stay at least 20 m from incubating and brooding hens.

The number of young reared by unmarked hens was determined using pointing dogs in August on a reference area of 836 ha where many of the marked hens nested. To make comparisons of marked and unmarked hens meaningful, reproductive success of marked hens was also checked with dogs in August.

All marked hens were captured on the 836-ha reference area, but six nested up to nine kilometres away. We combined the data for all marked hens, because reproductive success was similar for those nesting on and off the 836-ha area (0.9 vs 1.0 young/hen, $F_{1,18} = 0.22$, $P = 0.64$; effects of year and age controlled). Furthermore, reproductive success of unmarked hens on a second area eight kilometres distant from the reference area was similar to that of unmarked hens on the 836-ha area during the five years of counts (1.48 vs 1.54 young/hen, $\chi^2_1 = 0.11$, $P = 0.74$; effect of year controlled). One radio-marked hen attempted to breed in this second area.

The nests of radio-marked hens were located during incubation. Nest fate was checked either after hatching, or when nest failure was suspected (female found away from the nest on two consecutive checks). A nest was considered successful when ≥1 eggs hatched.

We employed General Linear Models with a Binomial Error distribution (BED) with a logit link function or a Poisson Error distribution (PED) with a log link function using GLIM software (NAG 1986), with stepwise backward deletions of non-significant terms, to compare reproductive parameters of different categories of hens (e.g. marked vs unmarked). When necessary, adjustment of the scale parameter was used to correct for overdispersion with the deviance ratio procedure (Aitkin, Anderson, Francis & Hinde 1989). In such cases, F statistics were used instead of χ^2-tests as suggested by Aitkin et al. (1989). The residual deviance/degree of freedom ratio C of the maximum model (including all interaction terms and main effects) was used to decide whether data were overdispersed ($C > 2$) or not ($C < 2$) (Aitkin et al. 1989, Crawley 1993).

We tested for differences in success in rearing a brood (hens with brood/total number of hens with and without broods) and for differences in the number of young reared per hen (total young/total number of hens with and without broods) of marked vs unmarked hens (effect of year controlled). In addition, we tested among marked hens for effects of age (yearling vs adult), year, and time of capture (hens marked in the current spring vs hens marked ≥6

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

months before laying) on success of nests (BED), success in rearing a brood (BED), number of young reared per hen including hens without brood (PED), and on the probability that a hen would renest after destruction of the first clutch (BED). Data from instrumented females that died before the end of the breeding season (31 August) were omitted.

Results

There were no significant between-year differences in the adult/yearling ratio of marked hens ($\chi^2_4 = 7.23$, $P = 0.13$). Hatching occurred at the end of June and early July (first nests) and in mid or late July (renests). Young were 2-7 weeks of age in early August. From 1991 to 1995, we monitored 14 hens captured as adults and seven captured as juveniles (autumn) or yearlings (spring). Of these 21 hens, 17 were monitored during a single breeding season, three during two and one during three seasons, corresponding to 26 marked-hen breeding seasons. Reproductive success (total number of young/total number of hens with or without brood) of hens monitored during two breeding seasons or more was not significantly different from that of hens monitored during a single breeding season ($F_{1,18} = 1.77$, $P = 0.20$; effects of year and age controlled). In 17 of the 26 marked-hen breeding seasons no young were reared because nests were destroyed by red fox *Vulpes vulpes* or marten *Martes martes* or *M. foina* and in three chicks were lost within one week of hatching. Six marked hens were accompanied by ≥1 chicks in mid-August. Each year from 1991 to 1995, we counted an average of 50 unmarked hens (range 37-69), 23 broods (11-44), and 83 juveniles (24-192) on the reference area.

Small samples of marked hens precluded testing for differences in annual mean brood size (number of young/brood) between successful marked and unmarked hens. For all years pooled, there was no detectable difference in the mean brood size of successful marked (3.3, N = 6) and unmarked hens (3.6, N = 114) (Mann-Whitney test, U = 314.0, P = 0.73, Table 2). However, after controlling for the effect of year, we found that marked hens raised fewer broods (0.23 vs 0.45 brood/hen, $\chi^2_1 = 4.96$, $P = 0.03$), and fewer young (0.77 vs 1.66 young/hen, $\chi^2_1 = 5.23$, $P = 0.02$) than unmarked hens (see Table 2).

Breeding performance of marked hens varied independently of age (all P values > 0.20) and year (all P values > 0.10), but hens captured in the current spring had lower nesting success (0.08 vs 0.57, $\chi^2_1 = 8.23$, $P = 0.004$) and raised fewer young (0.25 vs 1.2 young/hen, $F_{1,12} = 4.4$, $P = 0.058$) and fewer broods (0.08 vs 0.35 brood/hen, $\chi^2_1 = 4.56$, $P = 0.03$) than those marked ≥6 months before laying (Table 3). Moreover, females captured in the current spring renested less frequently in all years but 1992 (i.e. there was a significant effect of interaction between year and time of capture, $\chi^2_2 = 6.32$, $P = 0.04$) when the single successful female had been captured in the current spring and had renested (see Table 3). When the 1992 data were removed, the interaction was no longer significant ($P > 0.20$) but the effect of time of capture (hens marked in the current spring vs hens marked ≥6 months before) was still significant for all reproductive parameters considered (nest success: $\chi^2_1 = 15.59$, $P = 0.0001$; brood success: $\chi^2_1 = 9.54$, $P = 0.002$; number of young reared: $\chi^2_1 = 9.54$, $P = 0.002$; renest probability $\chi^2_1 = 7.78$, $P = 0.005$). In fact, only one of 12 females marked in the current spring raised a brood (see Table 3). All the other hens marked in the current spring initiated nests, but lost their first nests to predators within a few days of incubation, and did not renest (see Table 3).

Finally, hens marked ≥6 months before laying tended to raise fewer broods (0.35 vs 0.45 brood/hen) and fewer young (1.20 vs 1.66 young/hen) than unmarked hens but the differences were not significant (brood success: $\chi^2_1 = 0.61$, $P = 0.44$; number of young reared $\chi^2_1 = 1.18$, $P = 0.28$). In contrast females marked in the current spring raised significantly

Table 2. Reproductive parameters of black grouse hens with (marked) and without (unmarked) radio-transmitters in the Queyras, southern French Alps.

	Brood/hen		Brood size		Young/hen	
Year	Marked	Unmarked	Marked	Unmarked	Marked	Unmarked
1991	0.00 (0/2)	0.36 (18/50	-	3.1 (18)	0.00 (0/2)	1.11 (55/50)
1992	0.17 (1/6)	0.23 (11/48)	3.0 (1)	2.2 (11)	0.50 (3/6)	0.50 (24/48)
1993	0.50 (2/4)	0.46 (17/37)	2.0 (2)	3.1 (17)	1.00 (4/4)	1.43 (53/37)
1994	0.17 (1/6)	0.48 (24/50)	4.0 (1)	4.1 (24)	0.67 (4/6)	1.98 (99/50)
1995	0.25 (2/8)	0.64 (44/69)	4.5 (2)	4.4 (44)	1.12 (9/8)	2.76 (191/69)
1991-95	0.23 (6/26)	0.45 (114/254)	3.3 (6)	3.6 (114)	0.77 (20/26)	1.66 (422/254)

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Table 3. Reproductive parameters of black grouse hens marked in the current spring vs hens marked ≥6 months before spring, Queyras, southern French Alps.

	Hens marked in the current spring				Hens marked ≥6 months before spring			
Year	Nest success	Brood/hen	Renest probability	Young/hen	Nest success	Brood/hen	Renest probability	Young/hen
1991	-	-	-	-	0.00 (0/2)	0.00 (0/2)	0.00 (0/2)	0.00 (2)
1992	0.25 (1/4)	0.25 (1/4)	0.25 (1/4)	0.75 (4)	0.00 (0/2)	0.00 (0/2)	0.00 (0/2)	0.00 (2)
1993	0.00 (0/2)	0.00 (0/2)	0.00 (0/2)	0.00 (2)	1.00 (2/2)	1.00 (2/2)	1.00 (2/2)	2.00 (2)
1994	0.00 (0/3)	0.00 (0/3)	0.00 (0/3)	0.00 (3)	0.66 (2/3)	0.33 (1/3)	0.00 (0/1)	1.30 (3)
1995	0.00 (0/3)	0.00 (0/3)	0.00 (0/3)	0.00 (3)	0.80 (4/5)	0.40 (2/5)	0.50 (1/2)	1.80 (5)
1991-95	0.08 (1/12)	0.08 (1/12)	0.08 (1/12)	0.25 (12)	0.57 (8/14)	0.35 (5/14)	0.33 (3/9)	1.20 (14)

fewer broods than unmarked hens (0.08 vs 0.45, χ^2_1 = 7.13, P = 0.008) and fewer young in all years but 1992 (i.e. there was a significant effect of interaction between year and time of capture, χ^2_3 = 10.62, P = 0.013, see above and Table 2). When the 1992 data were removed, the interaction was no longer significant (χ^2_2 = 0.01, P = 0.99), but the effect of time of capture was still significant, that is marked hens captured in the current spring raised fewer broods (χ^2_1 = 11.52, P = 0.0007) and fewer young (χ^2_1 = 17.39, P = 0.0003) than unmarked hens (effect of year controlled).

Discussion

Low breeding success of hens marked in the current spring resulted largely from nest predation, and to a lesser extent from lower renesting frequency. In contrast, there were no detectable negative effects of radio-tracking, including possible handicaps caused by the radio-collar and monitoring activity, on reproductive parameters of hens marked ≥6 months before laying.

The results indicate that nests of hens captured just before or in the first days of laying suffered a higher risk of predation than nests of both unmarked hens and hens marked ≥6 months before laying. This increased risk could have been due to changes in the behaviour of hens because of the combined effects of stress of capture, handling, initial discomfort caused by the radio-collar, and persistent monitoring. Once the birds had adjusted to the transmitter, its presence alone may not have been a problem. The transmitters were relatively small, representing only about 2% of body weight. It has been generally accepted that transmitters weighing no more than 3% of the bird's body weight have no significant effects on survival or reproduction (but see Caccamise & Hedin 1985, Pennycuick, Fuller & McAllister 1989). In red grouse *Lagopus lagopus scoticus*, necklace transmitters weighing 2-2.5% of body weight apparently had no adverse effects on clutch size or hatching success (Thirgood, Redpath, Hudson, Hurley & Aebischer 1995).

Investigators may reduce nest success by increasing predation risk or nest desertion (Götmark 1992). Investigator disturbance probably does not entirely explain the differences we found in reproductive success between hens marked in spring and those marked earlier because nests of both groups were similarly monitored. But disturbance and monitoring could explain part of the difference between marked and unmarked hens. Among the marked hens, four (one was captured in the current spring) were accidentally flushed from their nest during incubation, two of which were successful (both marked ≥6 months before laying). The eggs of the other two were eaten by predators. One of these (which was marked ≥6 months before spring) apparently deserted before predation. Furthermore, we cannot totally eliminate the possibility that nest survival was compromised by observers approaching to within 20 m of nests several times during radio-tracking. On the other hand, two recent studies showed that investigator disturbance had a limited impact on nest success of rock ptarmigan *Lagopus mutus* (Cotter & Gratto 1995) and willow ptarmigan *L. lagopus* (Hannon, Martin, Thomas & Schieck 1993).

Dogs may have been more likely to find hens with broods than broodless hens, leading to a slight overestimation of reproductive success of unmarked hens. However, this does not explain the difference in reproductive success between females marked in the current spring and females marked ≥6 months before laying.

Previous radio-tracking studies on black grouse have not reported negative effects of radio-tracking on reproduction or survival (Angelstam 1984, Willebrand 1988), even though most hens were captured

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

on leks in spring. However, tolerance to capture and transmitters may differ between populations of the same species (Lance & Watson 1978).

Our results are in agreement with previous findings in other grouse species suggesting that hens are particularly sensitive to disturbance in the early stages of reproduction. For example, in red grouse reproductive success of hens equipped with back-pack radio-transmitters just before laying was poor, whereas hens reproduced normally when equipped halfway through incubation (Lance & Watson 1978). Moreover, Calvo & Furness (1992) showed that the most reported effect of radio-marking on birds was an initial discomfort lasting from a few minutes to a few weeks.

Previous studies generally reported few negative effects of radio-tracking on reproduction, but most focused only on radio-transmitter attachment or weight (e.g. Amlaner, Sibly & McCleery 1978, Warner & Etter 1983, White & Garrott 1990, Calvo & Furness 1992). Furthermore, many studies have been on captive females (Houston & Greenwood 1993). Others compared breeding success of females equipped with radio-transmitters to marked (ringed or back-tagged) or disturbed females (Boag, Watson & Parr 1973, Gilmer et al. 1974, Erikstad 1979, Taylor 1991, Foster, Forsman, Menslow, Miller, Reid, Wagner & Carey 1992, Cotter & Gratto 1995, Thirgood et al. 1995, Ward & Flint 1995). Most of these studies assessed effects of radio-marking on reproductive effort (Rotella et al. 1993) or on a short phase of the reproductive cycle (Pietz, Krapu, Greenwood & Lokemoen 1993) rather than on the number of young reared.

Our study has shown the most negative effect on reproduction of any radio-tracking study (including stress of capture, handling and persistent monitoring) of free-ranging wild birds (but see Foster et al. 1992). This is an important finding, because it has been previously suggested that radio-collars which are less restrictive and less conspicuous than transmitters mounted on harnesses or ponchos have minimal effects on behaviour, reproduction and survival (Thirgood et al. 1995). Unfortunately, we cannot draw general recommendations from our results, as the literature indicates there is no clear pattern of tolerance to radio-tracking. Each species, population, or class of individuals may react differently to radio-tracking. However, black grouse in the French Alps should not be fitted with radio-transmitters between several weeks before laying and sometime after hatching (see also White & Garrot 1990). Black grouse in the French Alps may be more sensitive than other black grouse populations (or grouse species) to the effects of marking, because of the high predation pressure on nests. In the French Alps, about 54% of nests of unmarked hens survive incubation (Ellison & Magnani 1985), whereas the survival rate during incubation in Finland is 71% (Lindén 1981). To obtain reliable data on reproductive success with necklace transmitters in the French Alps, hens should be marked several months before laying and nesting hens should never be approached closer than 20 m.

Management of bird species requires reliable data. Possible biases due to capture, handling, transmitter and monitoring should be systematically checked because the same methods may have different effects in different populations. Whenever possible, alternatives to marking (e.g. census techniques) should be the preferred method to estimate reproductive success. Otherwise, simulations (e.g. Leslie Matrix) should be used to assess the validity of estimated demographic parameters. Finally, researchers studying individual or population differences in life history traits should be aware of possible interactive effects of marking, e.g. yearlings could suffer more from marking than adults (Lance & Watson 1978).

Acknowledgements - we thank A. Bogtchalian, R. Corti, P. Guilhem, F. Kopko, P. Leonard, P. Longchamp, H. Pouderoux, D. Thiolière, T. Grzeganeck and J.P. Serres for field assistance. We are grateful to J. Blondel, O. Dehorter, M. Gibernau, M. Lambrechts, J.-D. Lebreton and two anonymous referees for comments on the manuscript, and to R. Julliard, R. Pradel and R. Nager for statistical advice. This work received financial support from: Office National de la Chasse, Fédération des Chasseurs des Hautes-Alpes, Société de Chasse de Ristolas, Commune de Ristolas, Conseil Général des Hautes-Alpes, Conseil Régional Provence-Alpes-Côte-d'Azur and Groupement d'Intérét Cynégétique du Queyras. The primary author received logistic support from the team 'Interactions Individus-Populations-Environnement' of the CEFE/CNRS Montpellier, France.

References

Aitkin, M., Anderson, D., Francis, B. & Hinde, J. 1989: Statistical modeling in GLIM. - Clarendon Press, Oxford, U.K., 374 pp.

Amlaner, C.J., Sibly, R. & McCleery, R. 1978: Effects of telemetry transmitter weight on breeding success in herring gulls. - Biotelemetry 5: 154-163.

Angelstam, P. 1984: Sexual and seasonal differences in

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

mortality of the black grouse (Tetrao tetrix) in boreal Sweden. - Ornis Scandinavica 15: 123-134.

Ascensio, E. 1983: Aspects climatologiques des départements de la région Provence Alpes Côte d'Azur. N° 2. - Ministère des Transports, Direction de la Météorologie, Boulogne Billancourt, 88 pp. (In French).

Boag, D.A. 1972: Effect of radio packages on behavior of captive red grouse. - Journal of Wildlife Management 36: 511-518.

Boag, D.A., Watson, A. & Parr, R. 1973: Radio marking versus back tabbing red grouse. - Journal of Wildlife Management 37: 410-412.

Burger, L.W., Jr., Ryan, M.R., Jones, D.P. & Wywialowski, A. 1991: Radio transmitters bias estimation of movements and survival. - Journal of Wildlife Management 55: 693-697.

Caccamise, D.F. & Hedin, R.S. 1985: An aerodynamic basis for selecting transmitters loads in birds. - Wilson Bulletin 97: 306-318.

Calvo, B. & Furness, R.W. 1992: A review of the use and the effects of marks and devices on birds. - Ringing and Migration 13: 129-151.

Cotter, R.C. & Gratto, C.J. 1995: Effect of nest and brood visits and radio transmitters on rock ptarmigan. - Journal of Wildlife Management 59: 93-98.

Crawley, M.J. 1993: GLIM for ecologists. - Blackwell Scientific Publications, Oxford, 379 pp.

Ellison, L.N. & Magnani, Y. 1985: Eléments de dynamique des population du tétras-lyre (Tetrao tetrix) dans les Alpes françaises. - Gibier Faune Sauvage 2: 63-84. (In French with English summary).

Erikstad, K.E. 1979: Effect of radio-packages on reproductive success of willow grouse. - Journal of Wildlife Management 43: 170-175.

Foster, C.C., Forsman, E.D., Menslow, E.C., Miller, G.S., Reid, J.A., Wagner, F.F. & Carey, A.B. 1992: Survival and reproduction of radio-marked adult spotted owls. - Journal of Wildlife Management 56: 91-95.

Gilmer, D.S., Ball, I.J., Cowardin, L.M. & Reichmann, J.H. 1974: Effect of radio packages on wild ducks. - Journal of Wildlife Management 38: 243-252.

Götmark, F. 1992: The effect of investigator disturbance on nesting birds. - Current Ornithology 9: 63-104.

Greenwood, R.J. & Sargeant, A.B. 1973: Influence of radio-packs on captive mallards and blue-winged teal. - Journal of Wildlife Management 37: 3-9.

Hannon, S.J., Martin, K., Thomas, L. & Schieck, J. 1993: Investigator disturbance and clutch predation in willow ptarmigan: methods for evaluating impact. - Journal of Field Ornithology 64: 75-80.

Helminen, M. 1963: Composition of the Finnish populations of capercaillie, (Tetrao urogallus), and black grouse, (Lyrurus tetrix), in the autumns of 1952-1961, as revealed by a study of wings. - Papers Game Research 23: 3-125.

Herzog, P. 1979: Effects of radio-marking on behavior, movements, and survival of spruce grouse. - Journal of Wildlife Management 43: 316-323.

Hines, J.E. & Zwickel, F.C. 1985: Influence of radio packages on young blue grouse. - Journal of Wildlife Management 44: 1050-1054.

Horton, G.I. & Causey, M.K. 1984: Brood abandonment by radio-tagged American woodcock hens. - Journal of Wildlife Management 48: 606-607.

Houston, R.A. & Greenwood, R.J. 1993: Effects of radio transmitters on nesting captive mallards. - Journal of Wildlife Management 57: 703-709.

Johnson, R.N. & Berner, A.H. 1980: Effect of radio transmitters on released cock pheasants. - Journal of Wildlife Management 44: 686-689.

Lance, A.N. & Watson, A. 1977: Further tests of radio-marking red grouse. - Journal of Wildlife Management 41: 579-582.

Lance, A.N. & Watson, A. 1978: Some strengths and limitations of radio-telemetry for research on grouse. - In: Lovel, T.W.I. (Ed.); Woodland Grouse Symposium. World Pheasant Association, Scotland, pp. 112-114.

Lindén, H. 1981: Estimation of juvenile mortality in the capercaillie, (Tetrao urogallus), and the black grouse, (Tetrao tetrix), from indirect evidence. - Finnish Game Research 39: 35-51.

Liscinsky, S.A. & Bailey, W.J.J. 1955: A modified shorebird trap for capturing woodcock and grouse. - Journal of Wildlife Management 19: 405-408.

Marcström, V., Kenward, R.E. & Karlbom, M. 1989: Survival of ring-necked pheasants with backpacks, necklaces and leg bands. - Journal of Wildlife Management 53: 808-810.

Marks, J.S. & Marks, V.S. 1987: Influence of radio collars on survival of sharp-tailed grouse. - Journal of Wildlife Management 51: 468-471.

McEwen, L.C. & Brown, R.L. 1966: Acute toxicity of dieldrin and malathion to wild sharp-tailed grouse. - Journal of Wildlife Management 30: 604-611.

NAG 1986: The Generalised Linear Interactive Modelling System. - The Royal Statistical Society, London, 306 pp.

Nenno, E.S. & William, M. 1979: Effects of radio packages on behavior of wild turkey hens. - Journal of Wildlife Management 43: 760-765.

Paquette, G.A., Devries, J.H., Emery, R.B., Howerter, D.W., Joynt, B.L. & Sankowski, T.P. 1997: Effects of transmitters on reproduction and survival of wild mallards. - Journal of Wildlife Management 61: 953-961.

Pekins, P.J. 1988: Effects of poncho-mounted radios on blue grouse. - Journal of Field Ornithology 59: 46-50.

Pennycuick, C.J., Fuller, M.R. & McAllister, L. 1989: Climbing performance of Harris' hawks (Parabuteo unicinctus) with added load: implications for muscles mechanics and radio tracking. - Journal of Experimental Biology 142: 17-21.

Pietz, P.J., Krapu, G.L., Greenwood, R.J. & Lokemoen, J.T. 1993: Effects of harness transmitters on behavior

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

and reproduction of wild mallards. - Journal of Wildlife Management 57: 696-703.

Ramakka, J.M. 1972: Effect of radio-tagging on breeding behavior of male woodcock. - Journal of Wildlife Management 36: 1309-1312.

Rotella, J.J., Howerter, D.W., Sankowski, T.P. & Devries, J.H. 1993: Nesting effort by wild mallards with 3 types of radio transmitters. - Journal of Wildlife Management 57: 690-695.

Small, R.J. & Rusch, D.H. 1985: Backpacks versus ponchos: survival and movements of radio-marked ruffed grouse. - Wildlife Society Bulletin 13: 163-165.

Taylor, I. 1991: Effects of nest inspections and radio-tagging on barn owl breeding success. - Journal of Wildlife Management 55: 312-315.

Thirgood, S.J., Redpath, S.M., Hudson, P.J., Hurley, M.M. & Aebischer, N.J. 1995: Effects of necklace radio transmitters on survival and breeding success of red grouse Lagopus lagopus scoticus. - Wildlife Biology 1: 121-126.

Ward, D.H. & Flint, P.L. 1995: Effect of harness-attached transmitters on premigration and reproduction of brant. - Journal of Wildlife Management 59: 39-46.

Warner, R.E. & Etter, S.L. 1983: Reproduction and survival of radio-marked hen ring-necked pheasant in Illinois. - Journal of Wildlife Management 47: 369-375.

White, G.C. & Garrot, R.A. 1990: Analysis of wildlife radio-tracking data. - Academic Press, San Diego, California, 383 pp.

Willebrand, T. 1988: Demography and ecology of a black grouse (Tetrao tetrix L.) population. - PhD Thesis, Uppsala, Sweden, 44 pp.

1903220x, 1998, 4, Downloaded from https://nsojournals.onlinelibrary.wiley.com/doi/10.2981/wlb.1998.023 by Cochrane France, Wiley Online Library on [07/03/2024]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License