ESTIMATING BROOD PRODUCTION AND CHICK SURVIVAL RATES OF GREY PARTRIDGES: AN EVALUATION

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ABSTRACT

AEBISCHER, N. J. and REITZ, F.: ESTIMATING BROOD PRODUCTION AND CHICK SURVIVAL RATES OF GREY PARTRIDGES: AN EVALUATION. Potts (1986, The Partridge: Pesticides, Predation and Conservation, Collins, London) described a method of estimating the parameters quantifying breeding success for the grey partridge *Perdix perdix* on the basis of autumn counts. We review his method and evaluate its accuracy against situations where the true values are known: an intensive study at Damerham, U.K. (1947-1959), two small radio-tracking studies in the U.K. (early 1980s), and a large-scale radio-tracking study in France (1995-1997). The method performed well when compared with the British data, which had been obtained from sites with low predator pressure. In France, estimated chick survival rates were also accurate after correcting for differences in brood size at hatching, even with sample sizes as low as two. The method proved not suitable to estimate hen survival rates in areas with a high density of harriers *Circus*. Elsewhere, the accuracy of the estimation of hen survival rates was generally good (making allowance for additional mortality caused by wearing radio transmitters), although it deteriorated for chick survival rates below 0.3.

1. INTRODUCTION

Any study of animal demography relies crucially on an accurate estimation of demographic parameters such as survival rates or breeding success. Over the last thirty years, sophisticated statistical methods have been developed to estimate such parameters from intensive studies, such as capture-mark-recapture for survival estimation (SEBER, 1982; BURNHAM *ET AL.*, 1987; POLLOCK *ET AL.*, 1990; LEBRETON *ET AL.*, 1992), or detailed nest monitoring for breeding success (HENSLER and NICHOLS, 1981; AEBISCHER, 1999). These methods require considerable time and effort to implement, and belong primarily to the domain of purpose-designed scientific research programmes.

Another source of demographic data, particularly in the field of wild game management, is the annual or biannual survey carried out for monitoring purposes and for determining harvest levels. Numbers of wintering geese, for example, are counted annually in several European countries to monitor population size (ROSE and SCOTT, 1994). In addition, the separate identification of adult and young geese during the counts gives an annual index of productivity, and a method of estimating annual survival rates (OWEN, 1982; EBBINGE, 1985; FOX *ET AL.*, 1989). This approach is much simpler than the previous one in terms of time and effort. Although potentially less rigorous and hence less accurate; it may nevertheless provide adequate estimates of some of the demographic parameters that are important for managers and, indeed, for population biologists (FOX *ET AL.*, 1989; EBBINGE, 1991).

For the grey partridge *Perdix perdix*, such surveys have been carried out routinely on European shooting estates after the cereal harvest (MIDDLETON, 1937; POTTS, 1986; BIRKAN and JACOB, 1988). As for geese, the separate identification of adult and young birds provides an annual index of productivity and an estimate of annual survival rates (MIDDLETON, 1935; BLANK and ASH, 1962; REITZ, 1992). Unlike geese, though, it is also possible to differentiate male and female adult grey partridges during the surveys (differences described in BIRKAN and JACOB, 1988), and to record individual brood sizes. POTTS (1980, 1986) used this further information to obtain a detailed breakdown of demographic parameters during the breeding period rather than simply an index of productivity, and proposed a series of formulae to do so. This paper uses data from intensive studies in the U.K. and in France for an evaluation of the accuracy of breeding parameters estimated using the Potts method.

2. METHODS

2.1.DEFINITIONS AND POTTS ESTIMATION OF DEMOGRAPHIC PARAMETERS

Originally a species of temperate grassy steppes, the grey partridge adapted readily to temperate agricultural landscapes and was once widespread across much of Europe. Since the 1950s, agricultural intensification has been the underlying cause of a decline of over 80% in most countries where the grey partridge occurs (POTTS, 1986; AEBISCHER and POTTS, 1994). A brief account of the life cycle of the grey partridge is as follows (POTTS, 1986; BIRKAN and JACOB, 1988). The species is monogamous. Birds pair in early spring, and nesting starts in May. The female alone incubates the eggs, while the male stands on guard. During the laying and incubation period, the hen is particularly vulnerable to ground predators such as the red fox *Vulpes vulpes*, while the eggs are attractive to corvids, mustelids, rats and other ground predators. The peak hatching period is the second half of June. Partridge chicks leave the nest only a few hours after hatching. They feed themselves, but initially require brooding by the parents to keep warm. During the first two weeks of life, the chick diet is predominantly invertebrate, then changes towards the mainly vegetable adult diet of seeds and green matter. Most chick mortality occurs within the first six weeks after hatching. In August, grey partridges form into coveys usually comprising a family group, often accompanied by one or more unsuccessful breeders. Shooting, if it occurs, takes place in autumn and early winter. Coveys persist through the winter, then break up in early spring as pairs form and the cycle starts again.

Aware of the above, POTTS (1980) identified six major demographic parameters that described the life cycle, and for which he proposed estimation formulae based on autumn count data. These parameters are defined below:

Hen survival rate: the proportion of spring females that survive the breeding season.

Clutch survival rate: the proportion of clutches that hatch at least one chick, after excluding clutches where the female died.

Brood production rate: the proportion of spring pairs that successfully hatch young. The brood production rate is the product of hen survival rate and clutch survival rate.

Chick survival rate: the proportion of chicks surviving for six weeks after hatching.

Shooting survival rate: the proportion of August partridges that survive the shooting season.

Overwinter change rate: the proportional change in number of females between the end of the shooting season and the following spring. This rate may include immigration, emigration, or both. It can also be calculated from August, in which case it includes shooting losses.

The estimation formulae proposed by POTTS used counts carried out after harvest, usually in late August. They required that in each observed covey, numbers of males, females and young be counted separately. The estimation of the breeding parameters revolved around the estimation of chick survival rate. POTTS recognized that the better the chick survival rate, the more young birds would be present on average in a covey. The relationship was complicated by the fact that the number of broods counted did not represent all broods that hatched, but only those where at least one chick survived. To take total brood losses into account, POTTS derived an empirical relationship between geometric mean brood size at count time and actual chick survival rate, using data from studies by JENKINS (1956) and BLANK and ASH (1962) **(Figure 1)**. The corresponding formula for the estimation of chick survival rate,

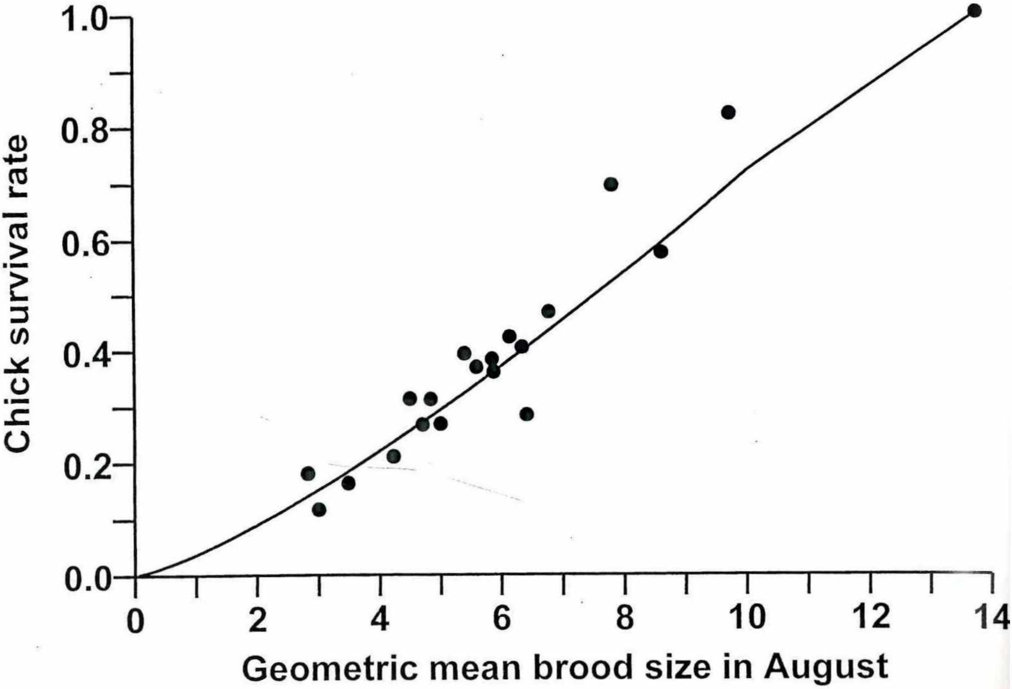

Figure 1: Empirical relationship between survival rates of grey partridge chicks and corresponding geometric mean brood sizes, based on U.K. data from JENKINS (1956) and the Damerham study; each point corresponds to a year. Source: POTTS (1986).

and the formulae that provide estimates of other demographic parameters, are presented in **Table 1.**

One major assumption underlying the validity of the formulae is that the number of August males represents the number of spring pairs (and hence the number of spring females). The argument for accepting this assumption is that the spring sex ratio is biased towards males, so that male losses during the breeding season reduce the number of spring males to the number of pairs. POTTS (1986, p. 42) showed that the assumption held for an intensive study area in the U.K.

Table 1: Formulae proposed by POTTS (1980, 1986) for the estimation of demographic parameters of the grey partridge, based on August covey counts.

Demographic parameter	Formula
Chick survival rate[1]	If geometric mean brood size $x \leq 10$: $0.03665\, x^{1.293}$ If geometric mean brood size $x > 10$: $x / 13.84$
Number of broods hatching:	(August young) / (chick survival rate) / 13.84
Brood production rate[1]:	(Broods hatching) / (August males)
Hen survival rate[1]:	(August females) / (August males)
Clutch survival rate[1]:	(Broods hatching) / (August females)
Overwinter change rate:	$(\text{Males in August})_{t+1}$ /(August females + ½ August young)$_t$

[1] Estimates are truncated if necessary to keep them between 0 and 1

Another assumption underlying the estimation of chick survival rate is that the average brood size at hatching is 13.84 (calculated from the averages of 27 U.K. studies: POTTS, 1986, p. 42). If this is not the case, then, as POTTS (1980) showed, the geometric mean brood size needs to be adjusted before the formula is applied, by multiplying by 13.84 and dividing by the correct brood size at hatching.

2.2. DAMERHAM AND OTHER U.K. STUDIES

The I.C.I Game Research Station carried out an intensive study of grey partridges from 1947 to 1959 on West Park estate at Damerham, in Hampshire, U.K. (BLANK and ASH, 1962; BLANK *ET AL.*, 1967). Out of a total area of 14.5 km^2, 5% was woodland, the rest was farmland that followed a mixed rotation of arable and grass such that about 50% was in cereals (POTTS, 1986). The estate employed five gamekeepers to manage the estate for partridges, including controlling the abundance of predators. The study involved complete censuses carried out in March, September and December, with a sample count of one-third to one-half of the March population in August. During these counts, birds in each covey were sexed and, if young birds were present and distinguishable (adult plumage is acquired after 12 weeks), aged as well. Large numbers of birds were individually marked, and more than half of the partridge nests were found each year; their outcome was closely monitored. These intensive data provided values for actual annual brood production rates and chick survival rates, while the raw data from the August counts were used to obtain matching estimates from the formulae in **Table 1.**

Two other intensive U.K. studies of grey partridges exist. GREEN (1984) monitored the fate of partridge broods with radio-tagged parents in two 10-km^2 areas of arable farmland in north-west Norfolk in 1980 and 1981. The adult females were tagged on the nest, and the survival of eight broods was assessed for 20 days from hatching. RANDS (1986) did likewise on a 11-km^2 arable farm in north-east Hampshire in 1984; he tracked 9 broods for 21 days from hatching. In both studies, gamekeepers were active on the areas concerned. The average survival rate of chicks up to three weeks of age was known exactly in both cases, and was given by (total number of chicks at three weeks) / (total number of chicks that hatched). It was compared with that calculated using POTTS' formula applied to the geometric mean of the brood sizes at three weeks.

2.3. FRENCH NATIONAL GREY PARTRIDGE STUDY

The Office National de la Chasse, the Union Nationale des Fédérations Départementales des Chasseurs and eight separate Fédérations Départementales des Chasseurs conducted a major study of grey partridge demography in northern and central France in 1995, 1996 and 1997 (REITZ, 1996). The study involved ten study sites, each between 20 and 150 km^2 in size, and at least 50 km apart. On average, about 30 females were radio-tagged on each site in each year in early spring, and monitored daily throughout the breeding season. The survival of the tagged females from 1 May to 31 August was calculated using the Kaplan-Meier method (POLLOCK *ET AL.*, 1989). If a tagged bird attempted to nest, the success or otherwise of incubation was recorded, as were the number of chicks at hatching and at six weeks. On the same sites, sample counts of the grey partridge stock were undertaken in August of each year; for each covey, the numbers of males, females and young were recorded. The radio-tagged birds provided exact data for each site and year on hen survival, clutch survival and chick survival rates. Using the formula in **Table 1**, matching chick survival rates were estimated from the geometric mean brood size at six weeks of all radiotagged females with broods. The August count data were used to estimate hen survival and clutch survival using the POTTS method for each site and year, for comparison with the values obtained from radiotagged birds.

At each site in each year, ancillary data were collected on harrier abundance in the summer (*Circus aeruginosus*, *C. cyaneus* and *C. pygargus* combined), by means of evening counts from a grid of fixed locations at the end of May and beginning of June. The counts were expressed as numbers of harriers per 10 km^2. For the present study, sites were classified into two categories according to whether the mean number over the three years was above 1 (harriers present) or below 1 (harriers absent). In 1996 and 1997, an index of mustelid abundance was obtained on each site by walking twice (two weeks apart) along 30 transects in May/June, and scoring each one as positive or negative for the presence of mustelid faeces. The index was the proportion of positives out of the 60 scores. Here, sites were classified into two categories according to whether the mean index value over the two years was above 0.3 (high mustelid density) or below 0.3 (low mustelid density).

3. RESULTS

3.1. EVALUATION OF POTTS' ESTIMATION: U.K. STUDIES

Using the data from Damerham, Figure 2 illustrates the excellent level of agreement between the chick survival rates observed by intensive monitoring of broods after hatching, and those estimated from August counts. That the points straddle the 1:1 line is not surprising, given that the formula for estimating chick survival rate was based partly on the Damerham data. What is noteworthy is that the average error in the estimates (vertical distance between each point and the 1:1 line) is small, even though the observed chick survival rates range from 0.11 to 0.77. Thus the mean difference between 11 estimated and observed rates was 0.012 (s.d. 0.052), indicating that approximately two-thirds of estimates were within 0.05 of the true chick survival rate. Sample sizes for the estimated rates lay between 49 and 148 depending on the year. The two points from the studies by GREEN and RANDS both appear below the 1:1 line, with departures of -0.04 and -0.06 respectively from the chick survival rates observed through radio-tracking.

The Damerham data also allow a comparison between 11 observed and estimated brood production rates (**Figure 3**). The average difference (bias) was -0.06, with a spread (s.d.) of 0.12, twice as high as that for chick-survival rate. The bias did not differ significantly from zero (t_9=1.83, P=0.100). For six of the years, the observed chick survival rates were below 0.3. All of the corresponding estimates of brood production rate were below the 1:1 line, two of them by over 0.2.

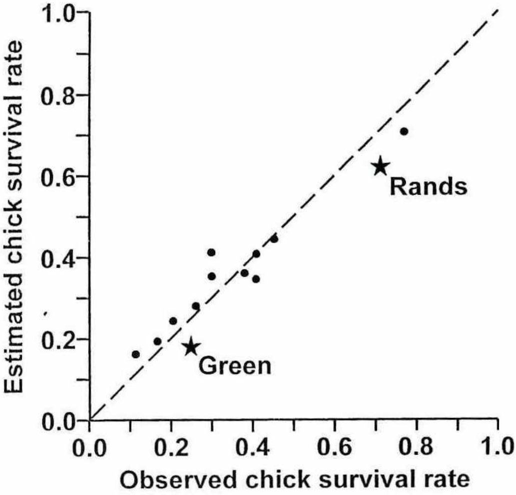

Figure 2: Comparison between estimated and observed chick survival rates of the grey partridge in the U.K.: data from the intensive study at Damerham (circles), and from two radio-tracking studies (stars) by GREEN (1984) and RANDS (1986). The dashed line represents 1:1 correspondence.

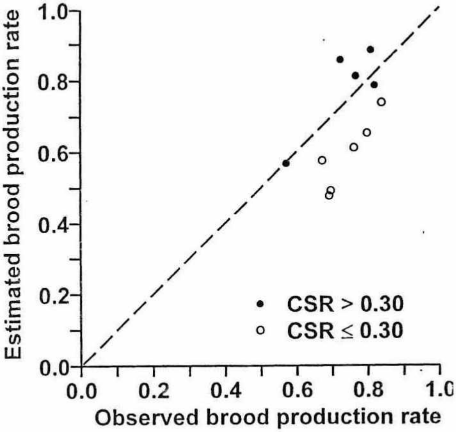

Figure 3: Comparison between estimated and observed brood production rates of the grey partridge in the U.K.: annual data from the intensive study at Damerham. The dashed line represents 1:1 correspondence. CSR = chick survival rate.

3.2. EVALUATION OF POTTS' ESTIMATION: FRENCH STUDY

Using data from broods with radio-tagged parents from the French study, observed annual chick survival rates were compared with estimated ones (**Figure 4**). The scatter from the 26 points was much greater than for the Damerham data (s.d. 0.18), but eight of the points were based on only one brood, and a further eight on two. When points based on only one brood were omitted, the scatter was reduced to 0.11. The mean difference between estimated and observed chick survival rates was -0.076, indicating significant bias (t_{16}=2.81, P=0.013).

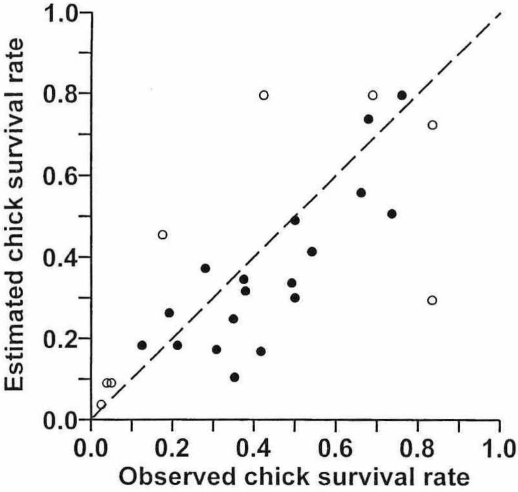

Figure 4: Comparison between estimated and observed chick survival rates of broods with radio-tagged parents in France: annual site data from the French National Grey Partridge Project. The dashed line represents 1:1 correspondence. Points based on only one six-week-old brood are open, those based on two or more are filled.

The POTTS method of estimating chick survival rate assumes an average brood size at hatching of 13.84. This assumption was not verified for the French radio-tracked broods, which averaged 11.79 chicks at hatching over the three years, with no significant effects of year or site (**Table 2**). In fact, the three annual averages in France were all lower than the 27

U.K. ones that contributed to the 13.84 (t_{28}=6.86, $P<0.001$). The estimated chick survival rates were therefore recalculated using the geometric mean brood sizes adjusted by multiplying them by 13.84/11.79 (**Figure 5**). This adjustment virtually eliminated the bias (mean difference between estimated and observed chick survival rates was 0.002, s.d. 0.13), and produced a good fit throughout the length of the 1:1 line. For comparison, the s.d. was 0.20 when adjusted values based on only one point were considered as well.

Table 2: Average brood sizes at hatching for grey partridges in the U.K. (POTTS, 1986) and for broods with radio-tagged parents in the French National Grey Partridge Project 1995-1997.

U.K. (POTTS, 1986, p. 46):
Average (± s.e.) of 27 studies 13.84±0.10

France (this study):

Year	Broods	Chicks hatched ± s.e.
1995	30	12.27±0.64
1996	38	11.84±0.62
1997	33	11.30±0.55
Overall	101	11.79±0.35

Two-way analysis of variance:
testing for an effect of year: $F_{2,89}$=2.07, P=0.132;
testing for an effect of site: $F_{9,89}$=1.50, P=0.160.

Estimated hen survival rates were almost without exception higher than observed ones obtained from radio-tagged females (**Figure 6**). The mean difference was 0.30 (n=29) with a s.d. of 0.19; the bias was significant (t_{27}=8.19, $P<0.001$). The points fell into two clusters, according to whether harriers were present or absent. In the presence of harriers, the mean difference between estimated and observed hen survival rates was 0.41 (s.d. 0.15), significantly greater than that in the absence of harriers (mean 0.14, s.d. 0.12, t_{27}=5.06, $P<0.001$). Taking into account the clustering associated with harrier presence, there was no evidence of a further effect of mustelid abundance ($F_{1,26}$=2.00, P=0.169).

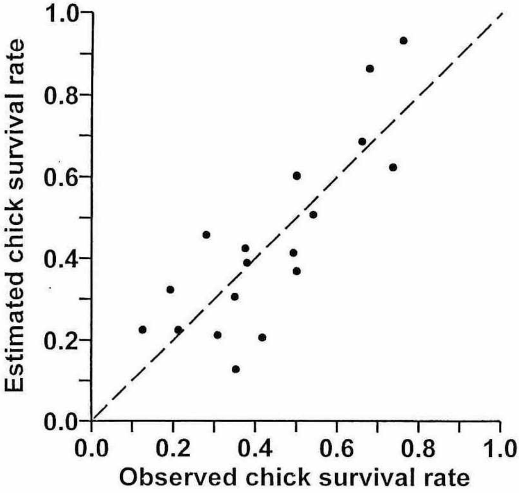

Figure 5: Comparison between estimated and observed chick survival rates of broods with radio-tagged parents in France: annual site data from the French National Grey Partridge Project, excluding points based on only one six-week-old brood. Estimates have been adjusted for a brood size at hatching of 11.79 instead of 13.84. The dashed line represents 1:1 correspondence.

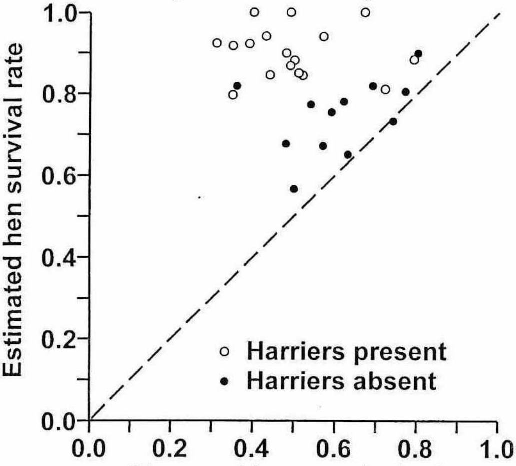

Figure 6: Comparison between estimated and observed hen survival rates in France: annual site data from the French National Grey Partridge Project. Observed rates were obtained from radio-tagged females, estimated ones from August counts. The dashed line represents 1:1 correspondence.

Estimated clutch survival rates were nearly all higher than those observed from radio-tagged females (**Figure** 7), and the bias was significant (mean difference 0.33, s.d. 0.24, t_{27}=7.24, P<0.001). The separation according to presence or absence of harriers was less marked than for hen survival, and not sufficient to show a significant difference (t_{27}=0.89, P=0.379). Nevertheless, in the absence of harriers there was a significant relationship between the estimated and the observed clutch survival rate ($F_{1,10}$=12.00, P=0.006), such that the slope differed significantly from one (t_{10}=5.53, P<001). No such relationship existed in the presence of harriers ($F_{1,15}$=0.07, P=0.790). There was no evidence of any clustering with regard to the abundance of mustelids ($F_{1,27}$=0.05, P=0.819).

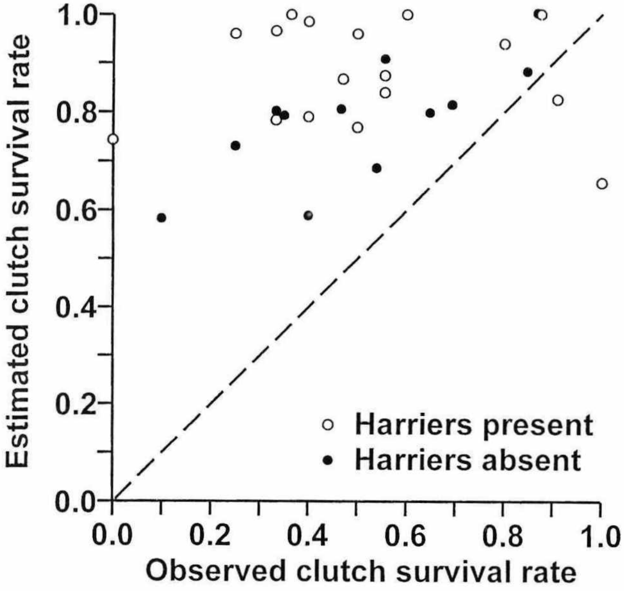

Figure 7: Comparison between estimated and observed clutch survival rates in France: annual site data from French National Grey Partridge Project. Observed rates were obtained from radio-tagged females, estimated ones from August counts. The dashed line represents 1:1 correspondence.

4. DISCUSSION

The empirical method of estimating chick survival rates from geometric mean brood sizes (**Figure 1, Table 1**) was found to perform remarkably well for all datasets, once the following factors had been taken into consideration:

(a) Brood size at hatching. Although there was high consistency in mean brood size at hatching across years and studies in the U.K. (POTTS, 1986), the value calculated for radio-tagged females in the French study was significantly lower than the U.K. average of 13.84, in line with the latitudinal trend noted by LACK (1947). As POTTS (1980) intimated, ignoring such differences can lead to positive or negative bias in the estimated chick survival rates, depending on whether the actual value is higher or lower than 13.84. Thus in the French study, actual brood size at hatching was 15% lower than the U.K. one, and resulted in a negative bias of –0.08. This bias disappeared when geometric mean brood size was adjusted upwards to compensate. As in the U.K., the French data indicated a high consistency in mean brood size at hatching across years and sites, implying that detailed knowledge of local variations in brood size at hatching is not necessary to apply the Potts method, so long as sufficient information on a broad regional scale is available to decide whether or not an adjustment is required.

(b) Survival period. The chick survival rates estimated for the two small U.K. radio-tracking studies were both lower (by 0.05 on average) than the observed ones. This was probably because they were estimated from broods aged three weeks instead of six weeks. Although most chick mortality occurs within the first 3-4 weeks after hatching (JENKINS, 1961; CARROLL *ET AL.*, 1990; REITZ and MAYOT, 1997), some additional losses would be expected during the next three weeks (e.g. PULLIAINEN, 1968). When applied to a mean brood size at three weeks, the formula in **Table 1** would return an estimated chick survival rate at six weeks, which should therefore be increased slightly to give one at three weeks. The observed difference is in line with what would be expected.

(c) Sample size. Not surprisingly, the accuracy of the estimation depends on the sample size used to calculate geometric mean brood size. POTTS (1986) recommended a minimum of ten broods for estimation purposes. Unexpectedly, even with sample sizes as low as two, the accuracy was good (**Figure 4**). The spread of the mean difference between estimated and observed fell from 0.20 when sample sizes of one were included, to 0.13 when they were excluded, while it was 0.05 when sample sizes were 49 or more with the Damerham data. Obviously, the higher the sample size the better, but the results imply that even in a situation where the stock is declining and it is increasingly difficult to find broods during the autumn counts, reasonable estimates of chick survival rate may still be obtained.

The Damerham study provided a direct comparison between estimated and observed brood production rates (**Figure 2**). The spread was similar to that recorded for the comparison of chick survival rates from the French study (excluding sample sizes of one), so can be considered good. Because the Damerham estate was well-keepered, observed brood production rates were all quite high (0.57-0.84), so that the adequacy of the method at low rates could not be assessed. The estimated values had a tendency to be more variable at low chick survival rates (below 0.3). This is because the calculation of estimated brood production rate involves division by the estimated chick survival rate (see **Table 1**); the lower the latter, the more even small differences between estimated and true chick survival rates become amplified in the process.. Given the fall in U.K. chick survival rates caused by the widespread use of herbicides (POTTS, 1977, 1980, 1986), and the more recently observed reduction associated with the use of summer insecticides (POTTS, 1990; AEBISCHER and POTTS, 1998), chick survival rates are now often lower than 0.3 (POTTS and AEBISCHER, 1995). The consequential effect on the accuracy of estimated brood production rates must therefore not be ignored, and such estimates should be treated cautiously.

The French study enabled separate comparisons between estimated and observed hen survival and clutch survival rates. Because the radio-tagging was directed at female partridges, it was not possible to apply the formulae in **Table 1** to the same birds that provided the observed rates (there was no equivalent of the number of August males). In consequence, the comparisons were not direct ones, but made use of August counts to evaluate estimated rates. This assumed that the observed rates from radio-tagged birds were representative of the population as a whole, and introduced an additional source of variation.

Nevertheless, the difference observed between sites with and without harriers was strikingly large. On sites without harriers, the spread was relatively low (similar to that recorded for the comparison of chick survival rates, excluding sample sizes of one). Although bias was present, it could be explained by increased mortality incurred because of the presence of the radio transmitters. With this interpretation, the bias of 0.14 represented the reduction in survival rate caused by wearing a transmitter. Such levels are compatible with what is known about radio effects on the wearer (e.g. WARNER and ETTER, 1983; MARKS and MARKS, 1987; CALVO and FURNESS, 1992). In the absence of harriers, therefore, it is likely that estimates of hen survival rates are good approximations to the actual ones.

In the presence of harriers, the use of the female:male ratio to estimate hen survival rates considerably overestimated the true rates. The reason was the relative shortage of males in the autumn counts. Indeed, in three cases there were more females than males, whereas the normal situation is for a surplus of males over females (BIRKAN and JACOB, 1988; REITZ, 1992). It seems likely that, as the male stands guard, he is more conspicuous than the female to foraging harriers, and hence more vulnerable. The additional male losses required to produce the observed difference in sex ratio may be evaluated from the ratio of the average estimated female survival rate in the absence of harriers to that in their presence. With a mean observed female survival rate of 0.46, and average biases of 0.14 for the estimated female survival rate in the absence of harriers and of 0.41 in their presence, this ratio was (0.46 + 0.14) / (0.46 + 0.41) = 0.69, i.e. the survival rate of males on sites with harriers needed to be 69% lower than on sites without them. Harrier diet is known to include adult gamebirds (SCHIPPER, 1973; UNDERHILL-DAY, 1985), but neither of these authors separated summer gamebirds into males and females. BRÜLL (1953) found, however, that 65% of grey partridges killed by goshawks were males: this may simply reflect the surplus of males over females in the population, or it may indicate greater vulnerability of males than females to raptors.

The distinction between sites with and without harriers is less clear in the comparison of estimated and observed clutch survival rates. On average there was a large positive bias, meaning that clutch survival rates obtained from radio-tagged females were consistently lower than those estimated from autumn counts. This is in line with BRO *ET AL.* (1999), who observed that, in general, overall chick production was lower for radio-tagged females than for control birds (BRO *ET AL.* were, however, not able to identify the reproductive stage when the difference occurred). In the absence of harriers, a significant relationship existed between estimated and observed clutch survival rates, albeit with a slope that was significantly less than one (**Figure** 7). This relationship could be the expression of a radio effect on clutch survival. In the presence of harriers, no such relationship was detected, possibly because harriers are recognized egg predators (CRAMP and SIMMONS, 1980).

In conclusion, chick survival rates can be reliably estimated from geometric mean brood sizes, provided that brood size at hatching is taken into account and sample sizes are at minimum two. The same holds for brood production rates, as long as chick survival rates are above 0.3. The evaluation of estimated hen and clutch survival rates is complicated by comparing observed values from radio-tagged females with estimated ones from August counts. No clear conclusion can be drawn for clutch survival rates, but hen survival rates seem well estimated in the absence of harriers.

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