DOI: 10.1080/03078698.2014.932614

Common but poorly known: information derived from 32 years of Coot (*Fulica atra*) ringing in the Camargue, Southern France

MATTHIEU GUILLEMAIN [1*], OLIVIER DEVINEAU [2], GERALDINE SIMON [3] & MICHEL GAUTHIER-CLERC [3]

[1] *Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune Migratrice, La Tour du Valat, Le Sambuc, 13200 Arles, France*.

[2] *Impasse de la Mairie, 30580 Fontareches*

[3] *Centre de Recherche de la Tour du Valat, Le Sambuc, F - 13200 Arles, France.*

***Running head**:* Guillemain et al.: Coot biometrics and survival.

Keywords: *Fulica atra*, ringing, biometrics, migration, survival rate

* Corresponding Author :

Matthieu Guillemain

Office National de la Chasse et de la Faune Sauvage, CNERA Avifaune migratrice, La Tour du Valat, Le Sambuc, F-13200 Arles, France.

Tel : +33. 490 97 28 79

Fax: +33 490 97 27 88

e-mail : matthieu.guillemain@oncfs.gouv.fr

SUMMARY

Rallidae are common and widespread, yet relatively poorly studied. We analysed the ringing data from more than 8,000 Common Coot *Fulica atra* accumulated between 1950 and 1982 in Camargue, Southern France, in terms of dynamics of their biometrics throughout the year, migratory pathways and annual survival rate. Mean monthly body mass and wing length indicate monthly differences, with birds captured in autumn and winter being heavier and larger than those captured in spring and summer. More than 950 ring recoveries were obtained, whose distribution across Europe and through time indicates a mixing of sedentary and migratory birds. The capture-recapture analysis indicated lower annual survival rate during the year following ringing, and greater survival in adults and in males. Mean survival rate over sex and age classes more than one year after ringing was 55%. This is somewhat lower than in other studies, and may be related to the importance of Coot hunting in Camargue, especially during the years of this study.

INTRODUCTION

The Rallidae are a family of very diverse bird species, among which some (e.g. Water rail *Rallus aquaticus*, hereafter Rail, Common Moorhen *Gallinula choloropus*, hereafter Moorhen and Common Coot *Fulica atra,* hereafter Coot) are particularly common and widespread (e.g. del Hoyo *et al* 1996). Several features of their behaviour have made Rallidae favourite study species within specific scientific domains: first, many of these species practice nest parasitism, cooperative nesting and/or have helpers, so the breeding ecology of Moorhen (e.g. Gibbons 1986, Elden 1987, McRae 1995, Forman 2005, Samraoui *et al*. 2012) and Coot (e.g. Samraoui & Samraoui 2007, Lu 2011, see also Lyon 1998 for American Coot *Fulica americana* and Jamieson *et al.* 2000 for Red-knobbed Coot *Fulica cristata*), in particular, has received much attention. Secondly, the young (e.g. in Coots *Fulica* spp.) and adults (e.g. in Rail or Moorhen) have peculiar head, shield or bill coloration, which lead to studies in the context of inter-individual signalling (e.g. Lyon *et al* 1994, Fenoglio *et al* 2002, Álvarez *et al* 2005). Finally, some species are kleptoparasites or, conversely, commensals with other waterbirds, so that their foraging ecology and role within waterbird communities have been the subject of many studies (e.g. Anderson 1974, Thomas 1982, Eddleman *et al* 1985, McKnight 1998, Källander 2005).

That some characteristics of the ecology of Rallidae have been the focus of so many studies contrasts with the poor knowledge available concerning the dynamics of their populations. Coots (*Fulica* spp.) often form large rafts, sometimes mixed with ducks (*Anatidae*), which has lead to the inclusion of these Rallidae into International Waterbird Censuses in the Palearctic; their population sizes are consequently well monitored, with current estimates suggesting stable or increasing trends in numbers in Europe (i.e. 1 750 000 individuals and stable in North-West Europe, 2 500 000 individuals and increasing in the

Black Sea/Mediterranean region, Wetlands International 2012). However, beside the population size, the demographic parameters of Rallidae are poorly known, with the exception of breeding success sometimes being quantified as part of nesting ecology studies (e.g. Fiala 1978, Gibbons 1986, Varo 2008). However, Coot have been captured and ringed in decent numbers over the last decades, either on purpose or as bycatch during duck ringing operations (e.g. O'Halloran 2002, Spina & Volponi 2008, Cepák *et al* 2008). This has been the case in Tour du Valat, Camargue, Southern France, where more than 8,000 Coot were captured in traps intended to catch ducks (Johnson 1975).

The aim of the present paper is to make this Camargue ringing data available and improve knowledge about this Rallidae, by i) providing the biometric data recorded at ringing, looking for possible patterns of change throughout the year, ii) documenting the migratory pathways of these birds by mapping their recovery locations, and iii) estimating their annual survival rate.

METHODS

A total of 8,337 Coot were caught in Tour du Valat between 1950 and 1982, mostly from the mid-1950s to the early 1970s (Figure 1). Catches occurred throughout the year, though more birds were trapped and ringed during the winter months (October to March, Figure 2). A season hereafter refers to the period between 1st August year n and 31st July year n+1, i.e. 1955 corresponds to the period between 1st August 1955 and 31st July 1956, for example.

These ringings led to 905 individuals (10.9%) being later recaptured at least once. The rings of 11.4% birds were eventually recovered. Most dead recoveries came from hunting (88.4%) or from birds found dead (6.8%).

Biometrics

Upon capture, the birds were weighed to the nearest gram and had their flattened wing length measured to the nearest mm, except on a few occasions when too many birds were simultaneously captured for detailed biometrics to be taken (see sample sizes in Figure 3). The age of Coot is extremely difficult to determine beyond a few weeks of age (Demongin 2013). Sexes are not possible to distinguish, apart from body measurement values, but there is a significant overlap between males and females (e.g. Visser 1976, Demongin 2013). Hence, a large proportion of the ringed birds remained of unidentified sex and age (Table 1). While testing for temporal (monthly) patterns of change in mean body mass and mean wing length, we considered 3 age classes (juveniles, adults and undetermined) and 3 sexes (males, females, undetermined) in order to be able to use the large proportion of individuals of undermined age/sex in the analysis. For consistency with the analysis of the distance of ring recoveries (see below), we also analysed the biometrics within a General Additive Models framework. However, because the explanatory variables were discrete for biometrics (i.e. age and sex classes, months), this was equivalent to using a General Linear Model. The best model was selected using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002).

Ring recoveries

Geographic coordinates of ring recoveries were available for 952 Coot. Recoveries of adults (n=293), first-year birds (n = 191) and birds of unknown age (n = 468) could be mapped separately. The distributions of mean recovery distances and mean recovery times from the Camargue ringing site were compared between age classes. Because these distributions did not differ between adults and first-year individuals (see results section), this factor (as well as sex, unlikely to profoundly affect ring recovery distances) were not included in the set of candidate models to explain changes in recovery distance from the ringing site. We used a Generalized Additive Model framework to model the effect of time since ringing (daysring) and date (daysring, expressed as 10-day periods since 1st August) on the recovery distance because the effect of date was expected to be non-linear. Indeed, an effect of date would indicate movements related to migration events, whereas an effect of time since ringing would rather indicate a diffusion from the ringing site. The best model was selected using the Akaike Information Criterion (AIC) (Burnham and Anderson 2002).

Annual survival rates

We modelled the survival of Coot using a multistate model with live recaptures (state A) and dead recoveries (state D). We fixed the survival parameters S and we used the transition parameters Ψ to estimate the actual survival (Gauthier & Lebreton 2008). For simplicity, we considered an annual interval based only on calendar years, i.e., ignoring the time of the year at which birds were ringed and/or recaptured or recovered. Because of difficulty to age and sex Coot in the field, a fairly large amount of birds were assigned to an unidentified group (coded I) for age at ringing and/or sex. We kept these unidentified groups alongside with juveniles (i.e., birds in their first year, coded "J") and adults (after first year, coded "A") for age, and males and females for sex (coded M and F). However, we tested candidate models in which all unidentified individuals were assigned to one of the usual groups (i.e., I=F or I=M for sex, and I=J or I=A for age at ringing). We also tested candidate models in which the first year following ringing (independently from age at ringing) was separated from subsequent years in order to account for the large number of birds that were never re-encountered again after ringing (variable "Time since Marking" or TSM). For all models, the probabilities of recapture and recovery were modelled as constant trough time and across groups to avoid over-parameterization given our relatively limited sample size. A total of 21 candidate models were tested using program MARK (White and Burnham, 1999) with the RMark interface (Laake 2013) and goodness-of-fit was assessed using program U-CARE (Choquet *et al* 2009) to estimate a coefficient of overdispersion, which we used to adjust the AIC, thus ranking models according to their QAICc value.

RESULTS

Biometrics

Mean wing length differed between months (Table 2, a) and an important part of the variation was explained by differences between sex and age classes, for which we kept all unidentified individuals in a third class. This makes it difficult to distinguish a clear pattern between males and females, or adults and juveniles. The pattern across months mostly consisted in shorter wings during spring and summer (Figure 3). Mean body mass was also strongly dependent on age/sex (with the same restriction as above on age/sex determination), and also differed between months with somewhat lighter individuals ringed during spring and summer (Table 2, b; Figure 3).

Ring recoveries

The maps of Coot recoveries is shown in Figure 4. Most recoveries occurred within a few days from ringing and at a short distance from the ringing site (Figure 5), with no significant difference in time or space distribution between adults and first-year birds, chicks excluded (Kolmogorov-Smirnov tests, both $P > 0.10$). Nevertheless, recoveries were scattered over a relatively clear south-west – north-east flyway, with some birds being recovered at considerable distances from the ringing site. Distance between ringing and recovery site was best explained by a model including a non-linear effect of date (i.e. 10-day periods since 1st August) and a non-linear effect of the time elapsed since ringing. Including non-linear predictors significantly improved the fit compared to using linear predictors (Table 2, c). While most Coot were recovered in or around Camargue, sometimes a considerable time after ringing, recovery distances were generally greater (though variable) in early autumn, late spring and summer, which is consistent with gradual migratory movements between Camargue winter quarters and distant breeding sites (Figure 6).

Survival analysis

The result of the model selection is presented in table 2. Adjusting the AIC with the estimated coefficient of overdispersion did not alter the model selection. The Coot data was best described by modelling survival as an interaction between groups (i.e., defined by sex and age at ringing, including unidentified individuals) and time since marking. This best-AIC model had an AIC-weight of 0.686, indicating a good support of the data. Differences between sexes were an important effect as sex was present in most top models. All best-AIC models also included the effect of time since marking on survival.

The best-AIC model provided estimates of survival for the first and subsequent years following ringing for each of the 9 groups defined by sex and age at banding (including unidentified individuals as separate groups for sex/age at ringing, Figure 7). Individuals of unidentified age generally had a survival rate intermediate between that of adults and juveniles, and individuals of unidentified sex had a survival rate intermediate between that of males and females (Figure 7). Survival was always lower during the year following ringing than during subsequent years (ca. 30% versus 55%). The survival of adults was generally higher than that of juveniles, and males had a higher survival rate than females (Figure 7). Most unexpectedly, the survival more than one year after ringing of birds ringed as juveniles was much higher for females than for males (71.89 vs. 41.39%). Interestingly, the difference between the survival of birds ringed as adults and as juveniles was apparent during the first year after ringing but vanished over the subsequent years (Figure 9).

DISCUSSION

A considerable number of Coot were ringed in Tour du Valat, Camargue, during more than 30 years. As such, the Tour du Valat dataset compares with the 8,700 Coot ringed until 2002 in the whole Czech Republic and Slovakia (Cepák *et al* 2008), and is twice larger than that for Belgium over a similar 30-years period (Del Marmol 1991).

Coot catches were mostly incidental in traps intended to catch ducks, so it is no surprise that the number of Coots ringed in Camargue was particularly large during the period of highest duck catching effort at this site, i.e. the 1960s (e.g. Guillemain *et al* 2009). Catches were especially numerous from October to March, highlighting that this dataset mostly consists of birds wintering in the area.

Coot ring recoveries were scattered over what appears to be a southwest-northeast migratory flyway, with birds being recovered further away along this flyway when more time has elapsed since ringing and, especially, during spring and summer. These recoveries spread along a broad line from Spain to Poland, which is consistent with the recoveries obtained from Czech and Slovak Coots (Cepák *et al* 2008), and from birds ringed or recovered in Italy (Spina & Volponi 2008). This also corresponds to the southernmost flyway described for this species by Del Marmol (1991). Despite this apparent migratory behaviour, many Coots were ringed or recovered locally in Camargue all year round. In support to Tamisier & Dehorter's (1999) statement, this suggests the population of Coot in Camargue in winter is composed of both migratory birds together with more sedentary individuals or local breeders (see also Cavé & Visser 1985 for the Netherlands, and Del Marmol 1991 for Belgium).

Therefore, it is difficult to analyse the changes in Coot biometrics due to potential heterogeneity between resident and migratory birds. The drops recorded in both wing length and body mass during spring and summer could be due to the inclusion of breeders and young individuals in the dataset during these months (e.g. young individuals not yet fully-developed, or incubating and moulting adults). It is unlikely that the greater wing length observed in winter is due to the inclusion of larger and heavier migrants. On the contrary, when the comparison was possible, non-local individuals tended to have shorter wings than local birds (Visser 1976). What is clear from figure 3 is that mean wing length, and more importantly, mean body mass are extremely stable throughout the winter (November to March). This strongly contrasts with other waterbirds which co-occur with Coot, e.g. dabbling ducks, where body mass typically peaks in mid-winter (e.g. Tamisier *et al* 1995). Such patterns of body mass changes are considered as fattening effort by the ducks as an insurance against potential adverse mid-winter weather, as well as the need to reduce feeding time in mid-winter to engage in mating behaviour instead (Tamisier *et al* 1995). This difference between Camargue ducks and Coot could be related with the mating system of Rallidae, which form pairs shortly before the breeding season (e.g. Cramp & Simmons 1980) while ducks pair earlier during winter (e.g. Tamisier *et al* 1995).

Annual survival rate of Coot more than one year after ringing was ca. 55% on average over sexes and age classes at ringing. This is much lower than the 70.1% annual survival rate provided for adult Coots in the Netherlands by Perdeck (1998). Such a difference in survival with northern countries is also apparent in the proportion of recoveries, i.e. 11.4% for the Camargue versus 5.6% in Belgium-ringed birds (Del Marmol 1991) and 6.8% for birds ringed in the UK (O'Halloran 2002). This may indicate a greater hunting pressure in Camargue during the ringing period. Indeed, communal hunts of Coot, where whole rafts were forced to take flight and birds shot in large numbers, were a traditional practice when the present data were collected (Mondain-Monval 2013). The South of France, and the Camargue in particular, still represents a large proportion of the national annual Coot hunting bag, but the total bag is clearly decreasing due to a declining interest to hunt this species (Trolliet 2000). Comparing the present Tour du Valat dataset with more modern Coot ringing data from Camargue could be a mean of testing the effect of hunting onto Coot populations, and to assess whether their survival rate has changed over the last 40 years.

A clear feature of the results was that survival rate during the year following ringing was lower for birds ringed as juveniles than for adults. In both cases the survival rate during the year of ringing was also much lower than during the following years. This is not surprising for birds ringed as juveniles, since a lower survival rate for first-year birds than for adult is common for waterbirds. This may be associated to the greater naivety of juvenile birds towards various mortality sources (including hunting and diseases, through a less developed immune system)(e.g. Owen & Black 1990). In this context, the ca. 25% survival rate recorded here for juvenile Coots during the first year after ringing is consistent with the 27% in Brinkhof *et al* (1997) and the 20.4% (mean over 15 years) in Cavé & Visser (1985), although considerably lower than the 37% in Perdeck (1998). The values provided in the first two studies were local survival probabilities, i.e. obtained from birds that were alive and present locally after one year. The similarity of these estimates with ours suggests that emigration rate may have been very low in both studies by Brinkhof *et al* and Cavé & Visser. The present results are also very similar to the 21% survival rate provided by Cavé (1977) for Coot ringed as pulli in the Netherlands and later shot. Both in the present study and in Cavé's results, the annual survival rate was much greater after the initial year following ringing (increasing to 55 and 75%, respectively), again highlighting the very significant improvement of survival with age. Surprisingly, the survival rate also increased dramatically between the year following ringing and the subsequent years for birds already adults at ringing, in a similar way as for birds ringed as juveniles. This may actually be a common phenomenon in Coot: Del Marmol

(1991) also recorded a greater mortality during the year following ringing, and attributed this to the Coot being mostly captured when they were facing energy needs (e.g. cold weather periods), so there would be more likely to die rapidly afterwards. If the birds could survive a harsh winter, their survival rate would increase again during the following years. The fact that the Camargue traps were baited with seeds to attract ducks could also have contributed to biasing the sample towards the most energy-stressed birds.

In most cases the survival rate of males was greater than that of females of the same age class. This again is a common feature of waterbird population dynamics (e.g. Devineau *et al* 2010 for Camargue-ringed Teal). In ducks, this is generally considered to reflect the greater investment of females in incubation and care of the young (which female ducks often perform alone), which is associated with greater predation risk (e.g. Sargeant & Raveling 1992). In Coot, however, both sexes spend a similar proportion of their time-budget incubating the eggs (e.g. Salathé & Boy 1987). Hence, the reason for the lower survival rate of females has to be different than in ducks, but remains unknown. It should be noted that Cavé & Visser (1985) provide very similar annual survival rates for male and female Coot (i.e. means of 57.6% and 55.8% over 15 years), although this was local survival at a breeding site, which cannot account for potential differences in emigration rates between males and females. Finally, why the pattern was reversed for juvenile-ringed birds several years after ringing (i.e. 71.8% in females, versus only 41.4% in males) was unexpected and remains unexplained.

Individuals of unidentified sex had a mean survival rate intermediate between that of males and females. This likely reflects the fact that these birds were a mixture of individuals of the two sexes. Similarly, individuals of unidentified age had a survival rate intermediate between that of adults and juveniles.

Although the present dataset is largely composed of incidental catches, it provides valuable information regarding the biometrics, movements and demographic parameters of Coot. Rallidae are widespread and common birds, and do represent a non-negligible game in some geographic areas (ca. 200 000 Coot, 150 000 Moorhen and 30 000 Rail shot annually in Europe after Hirschfeld & Heyd 2005). These birds are relatively easy to catch and can be marked with numbered collars or colour rings (e.g. Brinkhof *et al* 2002, Forman 2005, Martinez-Abraín *et al* 2007, Varo 2008). Beyond existing research schemes focusing on breeding systems or interspecific foraging interactions, a study relying on capture-mark-recapture of individually-marked birds at a wide geographic scale would represent a valuable research perspective to improve our knowledge of Rallidae.

ACKNOWLEDGEMENTS

We are most grateful to Luc Hoffmann, Hubert Kowalski, Heinz Hafner, Alan Johnson and the other people who ringed the Coot, Moorhen and Water Rail at the Tour du Valat over more than 30 years. We would especially like to thank Marc Lutz, Paul Isenmann and the Centre de Recherche sur la Biologie des Populations d'Oiseaux (Muséum National d'Histoire Naturelle, Paris) for their help while computerizing the Tour du Valat ringing database. The comments of two anonymous referees greatly helped improving an earlier version of the manuscript.

REFERENCES

Álvarez, F., Sánchez, C. & Angulo, S. (2005) The frontal shield of the moorhen: sex differences and relationship with body condition. *Ethology Ecology & Evolution* **17**, 135-148.

Anderson, M.G. (1974) American Coots feeding in association with Canvasbacks. *Wilson Bulletin* **86**, 462-463.

Brinkhof, M.W.G., Cavé, A.J. & Perdeck, A.C. (1997) The seasonal decline in the first-year survival of juvenile coots: an experimental approach. *Journal of Animal Ecology* **66**, 73-82.

Brinkhof, M.W.G., Cavé, A.J., Daan, S. & Perdeck, A.C. (2002) Timing of current reproduction directly affects future reproductive output in European Coots. *Evolution* **56**, 400-411.

Burnham, K. P. Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, NY, USA.

Cavé, A.J. (1977) Pitfalls in the estimation of age-dependent survival rates of birds from ringing and recovery data. *Vogelwarte* **29**, 160-171.

Cavé, A.J. & Visser, J. (1985) Winter severity and breeding bird numbers in a Coot population. *Ardea* **73**, 129-138.

Cepák, J., Klvaňa, P., Formánek, J., Horák, D., Jelínek, M., Schröpfer, L., Škopek, J. & Zárybnický, J. (2008) *Czech and Slovak bird migration atlas*. Aventinum, Praha, Czech Republic.

Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M. & Pradel, R. (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. *Ecography* **32**, 1071–1074.

Cramp, S. & Simmons, K.E.L. (1980) *Handbook of the birds of Europe, the Middle East and North Africa. Volume II. Hawks to Bustards*. Oxford University Press, Oxford.

Del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) (1996) *Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks*. Lynx Edicions, Barcelona.

Del Marmol, P. (1991) Interprétation des données Belges de baguage de la Foulque macroule, Fulica atra. *Le Gerfaut* **81**, 115-137.

Demongin, L. (2013) *Guide d'identification des oiseaux en main*. Laurent Demongin, Mortsel, Belgium.

Devineau, O., Guillemain, M., Johnson, A.R. & Lebreton, J.D. (2010) A comparison of green-winged teal *Anas crecca* survival and harvest between Europe and North America. *Wildlife Biology* **16**, 12-24.

Eddleman, W., Patterson, C.T; & Knopf, F.L. (1985) Interspecific relationships between American Coots and waterfowl during fall migration. *The Wilson Bulletin* **97**, 463-472.

Elden, S.F. (1987) When do helpers help ? Food availability and helping in the moorhen, *Gallinula chloropus*. *Behavioral Ecology and Sociobiology* **21**, 191-195.

Fenoglio, S., Cucco, M. & Malacarne, G. (2002) Bill colour and body condition in the Moorhen *Gallinula chloropus*. *Bird Study* **49**, 89-92.

Fiala, V. (1978) Contribution to the population dynamics and breeding biology of the Coot (*Fulica atra*). *Folia Zoologica* **27**, 349-369.

Forman, D.W. (2005) Laying plasticity in an avian brood parasite. *The Auk* **122**, 566-570.

Gauthier, G. & Lebreton, J-D. (2008) Analysis of band-recovery data in a multistate capture-recapture framework. *Canadian Journal of Statistics* **36**, 59-73.

Gibbons, D.W. (1986) Brood parasitism and cooperative nesting in the moorhen, *Gallinula chloropus*. *Behavioral Ecology and Sociobiology* **19**, 221-232.

Guillemain, M., Hearn, R., King, R., Gauthier-Clerc, M., Simon, G. & Caizergues, A. (2009) Comparing the migration of Eurasian Teal *Anas crecca* from two main wintering areas of Western Europe: a long-term study from Essex, England, and the Camargue, France. *Ringing & Migration* **24**, 273-276.

Hirschfeld, A. & Heyd, A. (2005) Mortality of migratory birds caused by hunting in Europe: bag statistics and proposals for the conservation of birds and animal welfare. *Berichte zum Vogelschutz* **42**, 47-74.

Jamieson, I.G., McRae, S.B., Simmons, R.E. & Trewby, M. (2000) High rates of conspecific brood parasitism and egg rejection in Coots and Moorhens in ephemeral wetlands in Namibia. *The Auk* **117**, 250-255.

Johnson, A.R. (1975) Station de baguage de Camargue. Compte rendu pour les années 1974 et 1975. *Comptes-Rendus d'Activité de la Station Biologique de la Tour du Valat* **21/22**, 28-34.

Källander, H. (2005) Commensal associations of waterbirds with feeding swans. *Waterbirds* **28**, 326-330.

Laake, J.L. (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle WA 98115.

Lu, X. (2011) Reproductive ecology of three Tibetan waterbird species, with special reference to life-history alterations along elevational gradients. *Zoological Studies* **50**, 192-202.

Lyon, B.E. (1998) Optimal clutch size and conspecific brood parasitism. *Nature* **392**, 380-383.

Lyon, B.E., Eadie, J.M. & Hamilton, L.D. (1994) Parental choice selects for ornamental plumage in American coot chicks. *Nature* **371**, 240-243.

Martinez-Abraín, A., Viedma, C., Bartolomé, M.A., Gómez, J.A. & Oro, D. (2007) Hunting sites as ecological traps for coots in southern Europe: implications for the conservation of a threatened species. *Endangered Species Research* **3**, 69-76.

McKnight, S.K. (1998) Effects of food abundance and environmental parameters on foraging behaviour of gadwalls and American coots in winter. *Canadian Journal of Zoology* **76**, 1993-1998.

McRae, S. B. (1995) Temporal variation in responses to intraspecific brood parasitism in the Moorhen. *Animal Behaviour* **49**, 1073-1088.

Mondain-Monval, J.Y. (2013) La diversité des gibiers et des pratiques. In *L'encyclopédie de la Camargue* (eds J. Blondel, G. Barrual & R. Vianet), pp 135-136. Buchet-Chastel, Paris.

O'Halloran, J. (2002) Common Coot (Coot) *Fulica atra*. In *The Migration Atlas: movements of the birds of Britain and Ireland* (eds Wernham, C.V., Toms M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R.), pp 266-268. T. & A.D. Poyser, London.

Owen, M. & Black, J.M. (1990) *Waterfowl Ecology*. Blackie, Glasgow, UK.

Perdeck, A.C. (1998) Poisson regression as a flexible alternative in the analysis of ring-recovery data. *EURING Newsletter* **2**, 30-36.

Salathé, T. & Boy, V. (1987) Territoriality and time budget of breeding Coots. *Wildfowl* **38**, 70-76.

Samraoui, F. & Samraoui, B. (2007) The reproductive ecology of the European coot (*Fulica atra* L.) in the Hauts Plateaux, north-eastern Algeria. *Waterbirds* **30**, 133-139.

Samraoui, F., Alfarhan, A. H. & Samraoui, B. (2012) Status and breeding ecology of the Common Moorhen *Gallinula chloropus* in Algeria. *Ostrich* **84,** 137-144.

Sargeant, A.B. & Raveling, D.G. (1992) Mortality during the breeding season. In *Ecology and Management of Breeding Waterfowl* (eds Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L.), pp 396–422. University of Minnesota Press, Minneapolis, USA.

Spina, F. & Volponi, S. (2008) *Atlante della Migrazione degli Uccelli in Italia. Vol. 1: non-Passeriformi*. ISPRA – MATTM, Roma, Italy.

Tamisier, A. & Dehorter, O. (1999) *Camargue, canards et foulques – fonctionnement et devenir d'un prestigieux quartier d'hiver*. Centre Ornithologique du Gard, Nîmes.

Tamisier, A., Allouche, L., Aubry, F. & Dehorter, O. (1995) Wintering strategies and breeding success : hypothesis for a trade-off in some waterfowl species. *Wildfowl* **46**, 76-88.

Thomas, G.J. (1982) Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. *Journal of Zoology (London)* **197,** 131-172.

Trolliet, B. (2000) Les Rallidés. Foulque macroule, poule d'eau, râle d'eau. In *Enquête nationale sur les tableaux de chasse à tir. Saison 1998/1999* (eds Landry, P. & Migot, P.), pp 150-159. Faune Sauvage 251.

Varo, N. (2008) Breeding biology of two sympatric coots with contrasting conservation status. *Bird Study* **55**, 314-320.

Visser, J. (1976) An evaluation of factors affecting wing length and its variability in the Coot *Fulica atra*. *Ardea* **64**, 1-21.

Wetlands International (2012) *Report on the conservation status of migratory waterbirds in the agreement area*. Agreement on the Conservation of African-Eurasian migratory waterbirds, 5th session of the meeting of the parties, La Rochelle, France.

White, G.C., & Burnham, K.P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**, 120–139.

Table 1. Sex and age distribution of individual Coot captured for ringing in Tour du Valat, Camargue, Southern France, between 1950 and 1982. Sex and age determination was based on morphometrics, except for the few cases when chicks were captured (numbers between brackets, also included in the total number of first-year birds).

SEX	**AGE CATEGORY**			
	Adults	**1st-year (Pulli)**	**Unknown**	**Total**
Males	831	239	713	1783
Females	512	336	1438	2286
Unknown	1515	1049 (79)	1704	4268
Total	2858	1624	3855	8337

Table 2. Model selection results for the analysis of wing length (a), body mass at ringing (b) and distance between ringing site and recovery location (c). Only the 3 Best-AIC models are presented for wing length and body mass. For recovery distance a fourth linear model is also presented. wing: wing length as measured at time of ringing, mass: body mass as measured at time of ringing, sex: includes females, males and undetermined, age: includes juveniles, adults and undetermined, mth: month of initial capture, distrecov: distance between ringing site and recovery location, daysring: number of days between ringing and ring recovery, period10d: ring recovery dates expressed as 10-days periods since August 1st, s(): denotes that smoother was applied and that the effect is non-linear (Generalized Additive Models). a), b) and c) are separate analyses.

	Model	**AIC**	**n**	**Adjusted R^2**	**Deviance explained (%)**
a	wing ~ sex + age + sex:age + mth	55079.43	8186	0.462	46.3
	wing ~ sex + age + mth	55104.28	8186	0.46	46.1
	wing ~ sex + age + sex:age	55118.47	8186	0.459	45.9
b	mass ~ sex + age + sex:age + mth	93562.14	7770	0.277	27.8
	mass ~ sex + age + mth	93584.37	7770	0.274	27.6
	mass ~ sex + age + sex:age	93694.16	7770	0.263	26.4
c	distrecov ~ s(daysring) + s(period10d)	11893.11	842	0.239	25.1
	distrecov ~ s(period10d)	12052.41	842	0.201	20.8
	distrecov ~ s(daysring)	11928.73	842	0.0727	7.9
	distrecov ~ daysring + period10d	12095.52	842	0.0197	2.2

Table 3. Result of the model selection process for the survival analysis for Coot. Only the first 7 models are presented here. For all models, the survival parameters S were fixed and the capture parameters p (probability of recapture pA and probability of recovery pD) were modelled as constant through time and across groups. The QAICs were adjusted using the estimated coefficient of overdispersion c-hat = 1.17. Group stands for age and sex (9 modalities for males, females, adults, juveniles and unidentified sex/age), TSM is time since marking (year following ringing versus subsequent years), Sex distinguishes males, females and individuals of unidentified sex, Age distinguishes adults, juveniles and individuals of unidentified age, SexIisF considered all individuals of unidentified sex as females.

Model	**DeltaQAICc**	**weight**	**QDeviance**	**npar**
Group * TSM	0.000	0.686	1915.229	20
Sex * TSM	3.597	0.114	1942.898	8
Sex + TSM	3.752	0.105	1947.060	6
SexIisF + TSM	5.319	0.480	1950.629	5
Group + TSM	6.554	0.259	1937.837	12
SexIisF * TSM	6.879	0.220	1950.186	6
Age * TSM	27.371	0.781	1966.672	8

FIGURE LEGENDS

Figure 1. Number of Common Coot captured and ringed per season (see text for how seasons were split) in Tour du Valat, Camargue, Southern France.

Figure 2. Monthly distribution of Coot catches in Tour du Valat, Camargue, Southern France between 1950 and 1982, expressed as percentage of total catch.

Figure 3. Mean wing length and body mass of Coot ringed in Tour du Valat, Camargue, Southern France, depending on month of capture. Vertical bars show standard errors, numbers in brackets are sample sizes, the month effect was statistically significant in both cases (see Table 2). Age classes are combined, including individuals of undetermined age because these represented close to 50% of the individuals.

Figure 4. Recoveries of Coot (white: first-year, black: adult, grey: age unknown at ringing) ringed in Tour du Valat, Camargue, southern France, between 1950 and 1982.

Figure 5. Time elapsed (top graph, limited to first 500 days) and distance travelled (bottom graph, limited to first 1000km) between ringing and ring recoveries of Coot initially captured in Tour du Valat, Camargue, between 1950 and 1982. The distributions for adults (black dots) and first-year birds (circles, individuals ringed as chicks excluded) did not differ significantly from each other in any of the two cases (see text). Data expressed per 10-day periods (100 standing for 91-100 days) and 10km classes of distance (100 standing for 91-100km).

Figure 6: Mean ring recovery distance for Coot from their Camargue ringing site depending on recovery date (expressed as 10-day periods since 1st August, i.e. beginning of the "season" as defined here). Vertical bars show standard errors, individuals from all age classes at ringing are included. See Table 2 for statistics.

Figure 7. Annual survival rate estimates for Coots ringed in Tour du Valat, Camargue, southern France, between 1950 and 1982. The first line on the X-axis refers to age at ringing (Adult, Unidentified or Juvenile), while the second line refers to sex (Female, Unidentified or Male). Black dots indicate survival rate during the year following ringing, grey dots the survival rate subsequent years. Vertical bars show standard errors.

Figure 1. Guillemain et al.

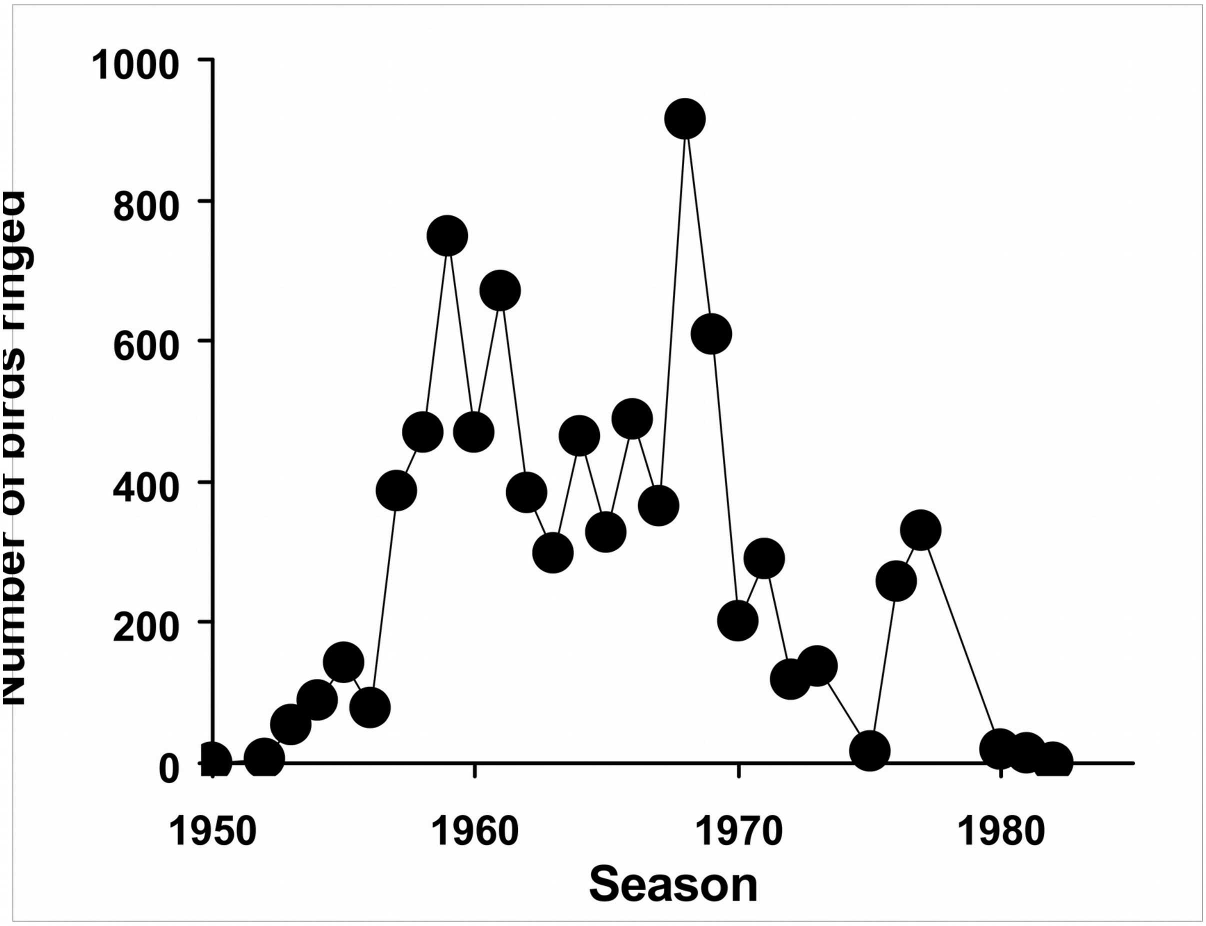

Figure 2. Guillemain et al.

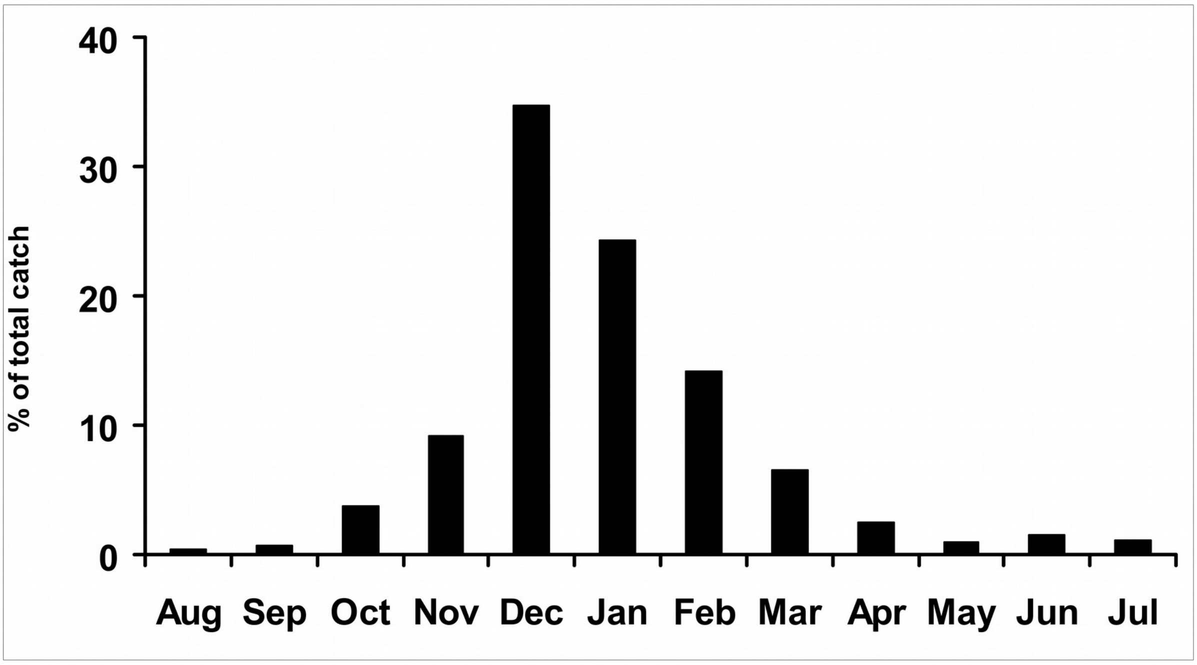

Figure 3. Guillemain et al.

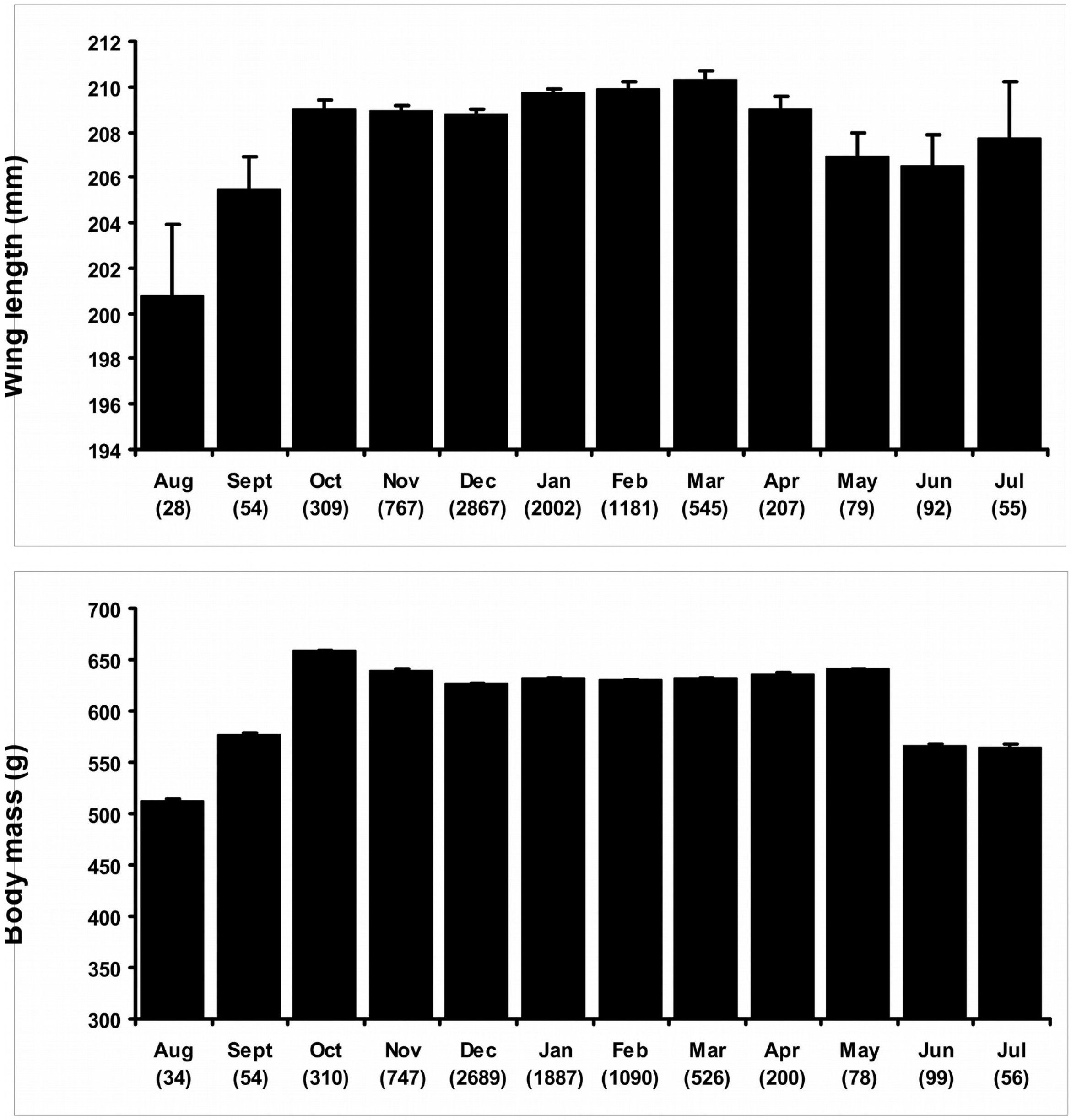

Figure 4. Guillemain et al.

Figure 5. Guillemain et al.

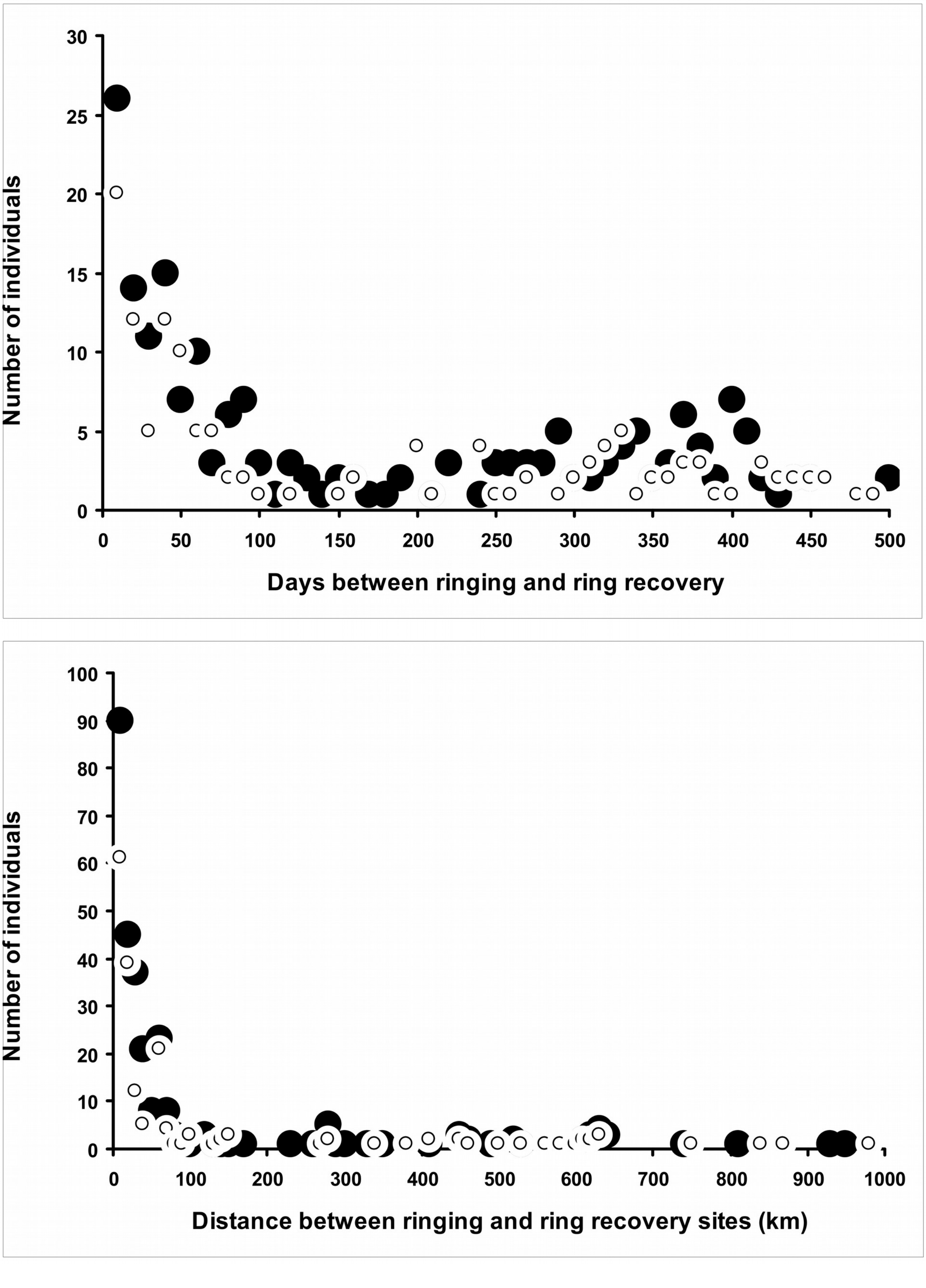

Figure 6. Guillemain et al.

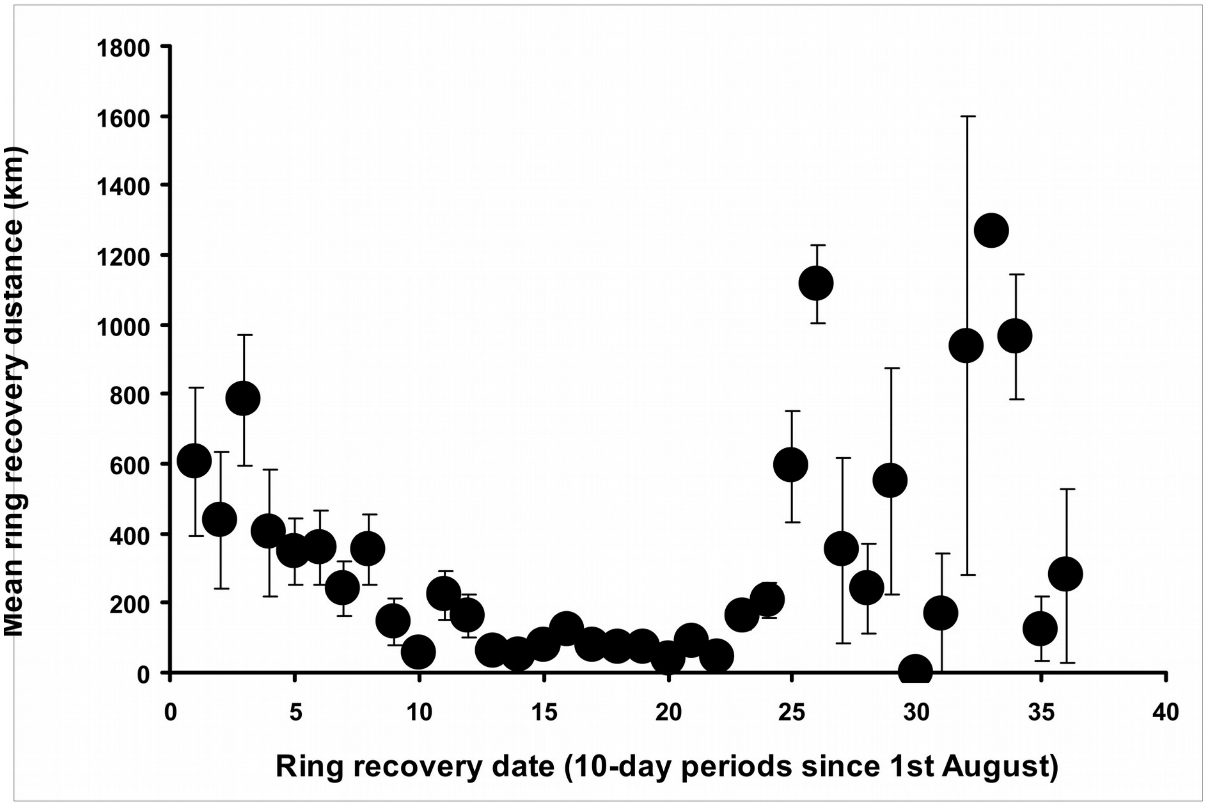

Figure 7. Guillemain et al.