

Habitat deterioration for waterfowl in French fishponds: insight from trends in Mallard *Anas platyrhynchos* breeding success

JOËL BROYER

Office Français de la Biodiversité (OFB), DRAS-Pôle ECLA, Station de la Dombes, Montfort, FR-01330 Birieux, France.
E-mail: joel.broyer@ofb.gouv.fr

Abstract

Declines in breeding success recently recorded for Pochard *Aythya ferina* nesting in French fishpond systems have raised questions about possible habitat change, which could be affecting other duck species as well. Here, declines in measures of Mallard *Anas platyrhynchos* breeding success are described for four main fishpond regions (Dombes, Brenne, Forez and Sologne), which provide important waterfowl breeding habitats in France. Significant declines were recorded in the ratios of broods to the total number of Mallard pairs for Dombes, Brenne and Sologne, and in the brood sizes of one-week-old families in Forez. No clear change was observed in duckling survival between 1–3 weeks of age. Annual breeding density of Mallard pairs varied unevenly across the study regions, decreasing in Sologne from 2004–2018 but increasing in Forez from 1992–2018. Such trends, similar to those previously recorded for the Pochard, support the hypothesis that habitat changes at French fishponds have affected the reproductive success of locally-breeding ducks. A possible influence of fish farming recession and the effect of Coypu *Myocastor coypus* feeding on nesting cover, are discussed.

Key words: fishpond, France, Mallard, recent trends, reproductive results.

In the mid-19th century, the Common Pochard *Aythya ferina* (hereafter Pochard) breeding range extended from Siberia to western Europe, reaching Ireland and Spain after a few decades, potentially driven by drought across its north-eastern breeding areas (Formosof 1934; Kalela 1946, 1949). More recently, in the last two decades, numbers have declined in many parts

of Europe including the southern parts of its range (Fox *et al.* 2016), probably due to declining productivity (Folliot 2018), demonstrated in its main French populations (Broyer 2019). In France, Pochard often breed in large pond complexes where extensive fish farming – which strongly influences local waterbird nesting conditions – has either become

abandoned (as in most of the Sologne and Forez), or is still currently in practice (as in Brenne and Dombes). Despite such contrasting local conditions, Pochard brood:pair ratios and brood sizes declined in all regions over the two last decades, yet breeding densities varied unevenly across the regions (Broyer 2019). Changes to fish farming management has been identified as a possible cause of Pochard decline in Europe (Fox *et al.* 2016), but results from France suggests a more complex explanation for declines in productivity. Detecting similar trends in other waterfowl species across French fishpond systems would confirm the hypothesis of general habitat change, and might help us to understand the Pochard decline.

In this analysis, trends in density and breeding productivity are examined for the other most abundant duck species, the Mallard *Anas platyrhynchos*, over the same time period as for Pochard. Both species breed on the same water bodies but show different migration patterns and wintering distribution. Similar patterns of falling Mallard reproductive success would support the hypothesis that the decline observed in Pochard productivity at French fishponds are the results of changes in habitat quality at these sites.

Methods

Study areas

The study was carried out in Brenne (1999–2018) and Sologne (2004–2018 except 2010–2012) in central France, and in Dombes (1994–2018) and Forez (1992–2018) in the east of the country (Fig. 1). Carp *Cyprinus*

carpio has been the major contributor to fish farm production in all regions, but many ponds in Sologne have now been abandoned for several decades; only 25% of the 3,000 existing ponds are still regularly stocked with fish and harvested. Aquaculture in Forez (250 ponds) declined mainly during the 1990s. In the two other regions (> 1,000 ponds each), fish farming is more persistent, but with a significant decrease in the level of pond fertilisation by fish farmers (nitrogen spreading or cow manure application) in Dombes from the early 1990s, and in Brenne a decade later.

Except in the densely wooded Sologne, fish ponds are surrounded mainly by arable crops or pastures. Agriculture in pond watersheds is more intensive in Dombes, where massive conversion of grassland to cereal crops since the 1970s has had an adverse effect on breeding conditions for duck (Tournier 1990; Broyer 2000), resulting in increased clutch predation because of a concentration of nests along pond edges (Broyer 2009). Duck harvest by hunters at the start of the open season probably also impinges on local populations. Although precise statistics are lacking, a national survey in winter 2013/14 found little change in the annual Mallard hunting bag compared to 15 years earlier (Guillemain *et al.* 2017), and hunting pressure in the study regions are considered to be stable or slightly decreasing. A striking change to pond ecosystem in all regions has been the rapid expansion of the Coypu *Myocastor coypus* during the 1990s which feed on aquatic vegetation, resulting in a dramatic reduction in the abundance of emergent vegetation at all sites (Curtet *et al.* 2008).

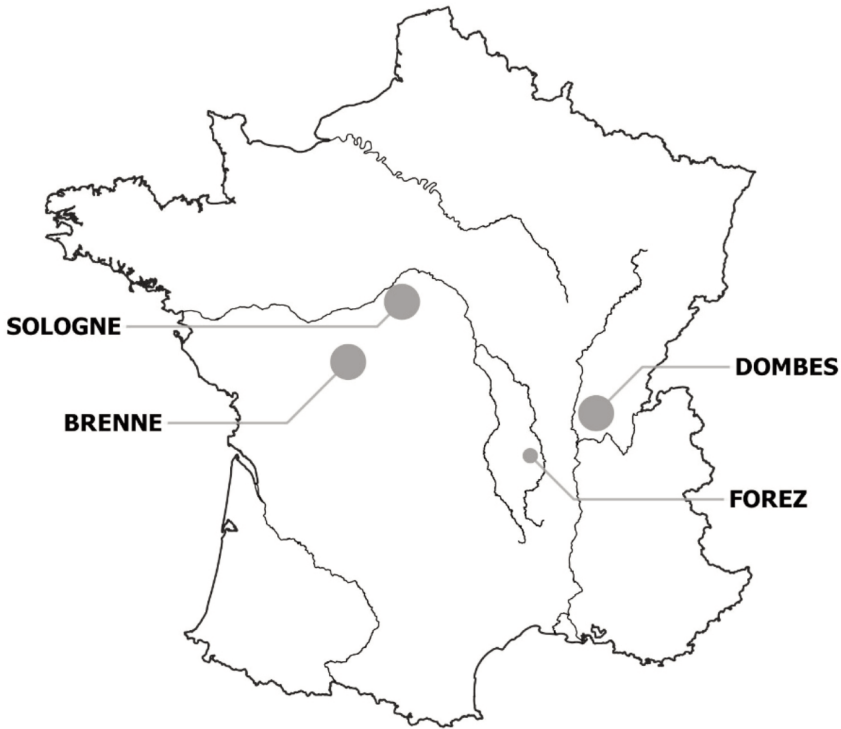


Figure 1. Map of France showing the location of the four study sites.

Ponds sampled in each region

Breeding Mallards were studied at 80 ponds in Dombes (mean \pm s.d. surface area $S = 13.9 \text{ ha} \pm 13.3$), 57 in Brenne ($S = 10.9 \text{ ha} \pm 9.1$), 60 in Sologne ($S = 8.9 \text{ ha} \pm 8.1$) and 60 in Forez ($S = 7.4 \text{ ha} \pm 7.6$). The ponds sampled were consistent from year to year, except in Dombes where each pond is left empty and ploughed for cereal cultivation every fourth year. Roads or tracks providing motor vehicle access were used to contribute routes to five transects established for each region, each of which could be covered within a day, so that all ponds were visited within the same week. Routes were planned to ensure that the most representative parts

of the study regions were traversed, and that typically managed fishponds were included in the surveys. The distances to reach all studied ponds of each transect were 5–8 km, covered by car. Distances between neighbouring transects were usually 3–5 km.

Duck censuses

Mallard adults and broods were counted every week from mid-April to the end of July, at the same time as surveys made of Pochard and other waterbirds in the same study areas (Broyer 2019). On each occasion, this involved making one slow but comprehensive scan of the whole area of the pond, using a $\times 40$ telescope.

Observations were limited to mornings and late afternoons to avoid the hottest part of the day when birds may seek shelter within vegetation cover. Time spent on each pond was proportional to the surface area to be surveyed and to the abundance of aquatic vegetation likely to constitute visual obstacles. Pairs, isolated adults and groups were recorded separately during the scan, with brood size and the age of ducklings (in weeks) also recorded systematically. Brood age was determined by comparing the body lengths of the ducklings to the body length of the female (following Fournier & Cordonnier 1982). The contemporaneous field work had to rely on different observers across regions, and usually also from year to year, which could introduce an observer effect in detection of the birds. The same well-trained observer, however, did all weekly counts in each region for a given year, while the frequency of visits would also help to reduce any bias in the results.

Data analysis

Pair density

The density of Mallard pairs determined from ground counts may be considered only an approximation of the absolute numbers of breeding pairs per pond because of movement of individuals to and from the site. For many research and monitoring applications, however, the level of error can be assumed to be low, because breeding pairs restrict their activity during the pre-nesting, laying and early incubation periods (Rotella *et al.* 1995). The number of Mallard pairs per pond were estimated during the pre-nesting and early incubation periods, *i.e.* between April 15 and May 25 (at least

5 visits). Pairs and isolated adults were recorded separately in each of the weekly counts and large groups of males, females or both sexes were normally not considered for assessing pair numbers per pond. For each weekly count in each pond, we added to the observed number of pairs, either lone females (considered to be on a short recess from incubation), or males alone and in small groups (< 5) thought to be paired birds where the female had started incubation, and retained the highest of these two additions. As a rule, the number of pairs per pond used in the analyses corresponded to the highest number recorded at least three times across the study period (April 15–May 25) that year. Of course, we cannot know with certainty that the number of pairs assigned by this method to a given pond eventually nested there.

Defining comparative indices of pair numbers per unit area was complicated by strong interactions between the pond's surface area and Mallard abundance. Relationships between the pond's surface area and: 1) pair number, 2) pair number divided by pond surface area, or 3) pair number divided by the square root of pond surface area, were compared in each study region for 3 years selected at random. Pair number was related (linear regressions with $P < 0.05$) to pond surface area in 89% of selected annual samples, in 78% once divided by pond surface area, and in 11% when divided by the square root of pond surface area. The number of pairs therefore was divided by the square root of the pond's surface area to offset this effect, which probably reflects increasing availability of nesting habitat along pond perimeters.

Mallard pair density here was taken as the annual mean value for each sample.

Brood:pair ratio

The ratio of the number of broods to the number of pairs was calculated to generate an overall annual index for each study region, based on the sum of the number of pairs recorded at each pond in the region. Because broods may move between neighbouring ponds, only ≤ 2 -week-old broods were considered in determining the number of broods, in order to limit the risk of double counting. Brood number was the sum of all ≤ 1 -week-old broods recorded at different dates throughout the sample and of 2-week-old broods provided that no ≤ 1 -week-old broods of same or bigger size were observed in the same pond or in a nearby pond in the preceding weekly count (as for Broyer 2019).

Brood size and duckling loss in early stages of growth

In order to determine the loss of ducklings after hatching, duckling numbers at ≤ 1 week old were used for assessing the initial mean brood size on hatching. Because duck brood sizes decrease at French fishponds mainly during the first 3 weeks after post-hatch (Broyer 2002), duckling losses at the ponds included in the study were then estimated as the percentage difference between ducklings counted at 1-week-old stage and those at 3 weeks old. To limit the possible error introduced by broods being present but undetected, the 1-week-old brood number was considered as being equal to 1-week-old + 2-week-old observed for the first time, and 3-week-old brood number was equal to

3-week-old + 4-week-old broods where the latter were not observed at 3 weeks of age. This method assumed that any ingress of broods into the ponds being monitored was counterbalanced by a similar egress of the same number to water bodies away from the study sites. Such conditions were expected considering that ponds in transects did not *a priori* differ from the surrounding ones.

Statistical analysis

Generalized linear mixed models (GLMMs) in Program R (R 64 3.0.3., with package lme4) were used to analyse trends in the demographic variables (using annual regional means recorded at the sampled ponds), with “year” included as an explanatory variable and “region” as a random effect in the model. The distribution of all dependent variables permitted the use of a Gaussian error term. AIC scores for each of the models were compared to the scores of the respective null models and confirmed by a graphical analysis. In cases with $\Delta\text{AIC} \leq 2$, or where the AIC was higher than the score of the null model, each regional trend was described individually by the best curve fitting (highest r^2) from a linear, quadratic or cubic regression. The mean values of each variable in the first five years and the last five years of the study are given to illustrate the magnitude of the change over time.

Results

The GLMMs failed to identify clear global trends over time across the four study regions in pair density, duckling losses and brood size, with AIC higher than the scores of the respective null models in each case

Table 1. Results of GLMMs explaining the variation with time of Mallard pair density, brood size, brood:pair ratio and duckling loss, with “region” included as a random effect in the models. AIC comparisons are with the respective null models.

	Estimate (\pm s.e.)	<i>t</i> -value	d.f.	AIC	AIC (null)	Δ AIC
Pair density	0.0045 (\pm 0.0047)	0.963	74	52.82	42.84	+9.98
Brood size	-0.0393 (\pm 0.0128)	-3.061	78	214.72	214.79	+0.07
Brood:pair ratio	-0.0106 (\pm 0.0021)	-5.125	73	-71.25	-61.12	-10.13
Duckling loss	-0.0029 (\pm 0.0024)	-1.192	75	-50.63	-61.42	+10.80

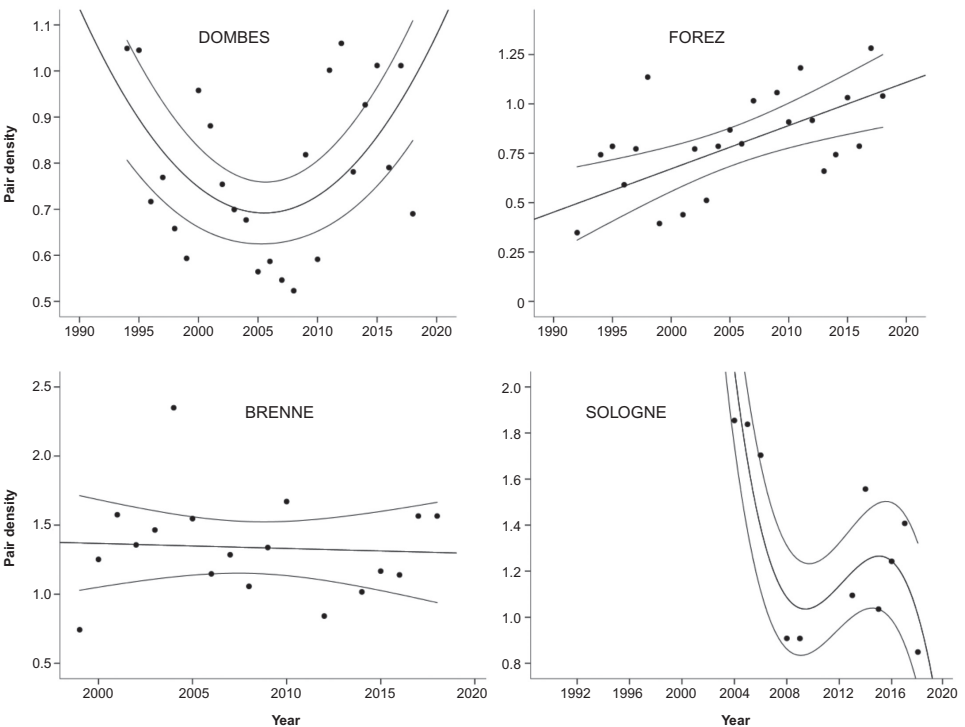


Figure 2. Regional trends in Mallard pair density (regression curves with 95% confidence intervals), in Dombes (quadratic regression: $r^2_{24} = 0.246$, $P = 0.045$), Brenne ($r^2_{17} = 0.004$, $P = 0.81$, n.s.), Forez (linear regression: $r^2_{23} = 0.316$, $P = 0.004$), and Sologne (cubic regression: $r^2_{10} = 0.661$, $P = 0.045$).

(Table 1). Specific regional variation with time was nevertheless recorded in pair density (Fig. 2). The best fit regression models were a quadratic regression in Dombes ($r^2_{24} = 0.246$, $P = 0.045$) showing a sharp decline between 1994 and 2010 followed by a rapid recovery afterwards; a positive linear regression in Forez ($r^2_{23} = 0.316$, $P = 0.004$); no clear variation in Brenne ($r^2_{17} = 0.004$, $P = 0.81$); and a cubic regression in Sologne ($r^2_{10} = 0.661$, $P = 0.045$) with a sudden collapse after 2006 (Fig. 2). No trend in any region was recorded in duckling losses between the first and third weeks after hatching ($r^2 < 0.05$, n.s. in each case, except in Sologne where $r^2_{10} = 0.141$,

$P = 0.25$, n.s.). Similarly, brood size did not vary over time in Dombes, Brenne and Sologne ($r^2 \leq 0.1$, $P > 0.3$, n.s. in each case) but decreased in Forez ($r^2_{23} = 0.375$, $P = 0.001$) (Fig. 3).

There was however clear evidence for a general trend in the brood:pair ratio ($t_{77} = -5.125$, $\Delta AIC = -10.13$ in comparison with the null model; Table 1). Graphical analysis indicated a common declining trend across the study regions ($r^2 \geq 0.4$) except in Forez ($r^2_{21} = 0.038$) (Fig. 4).

Comparing the mean values for these parameters in the first five years and last five years of the study in each region (Table 2) provides further insight into the extent

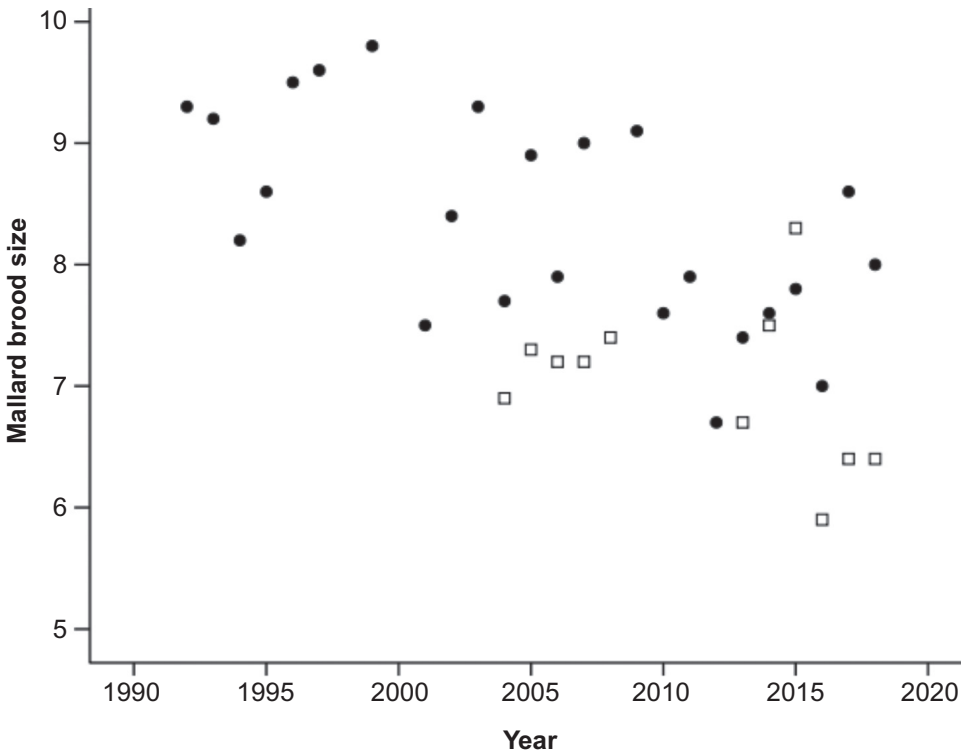


Figure 3. Trends in Mallard brood size in Forez (black circles) and in Sologne (white squares).

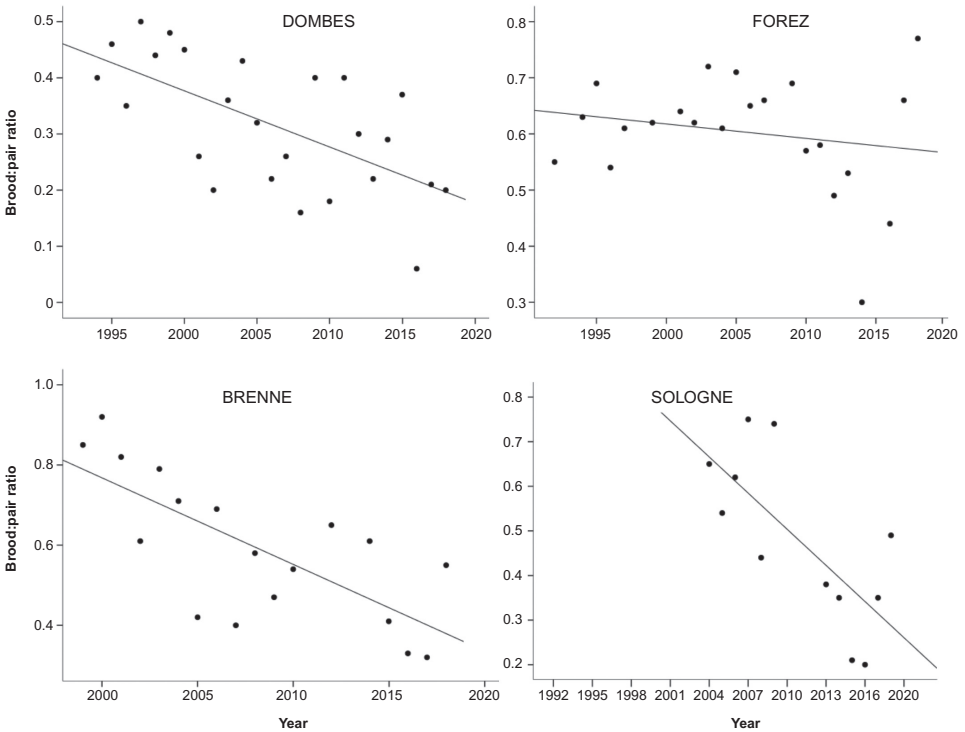


Figure 4. Trends in Mallard brood:pair ratio in Dombes ($r^2_{24} = 0.397$, $P = 0.001$), Brenne ($r^2_{17} = 0.534$, $P = 0.001$), Forez ($r^2_{21} = 0.038$, $P = 0.38$, n.s.) and Sologne ($r^2_{11} = 0.521$, $P = 0.008$).

of change in different regions over time. This confirmed the decrease in the brood:pair ratio, by *c.* 50% in each region except in Forez where the ratio remained quite stable. Conversely, the mean brood size for 1-week-old broods in Forez decreased by > 1 chick/brood (on average) between the two observation periods whereas, in the other study regions, there were no clear difference in brood sizes between the first and last five years of the study. Pair density increased in Forez by 51% and decreased in Sologne by 22%, but there was no overall change recorded in Dombes and Brenne.

Discussion

Variation in Mallard pair density at French fishpond complexes recorded across the study period was region specific and showed no common trend (as in the case of the Pochard). Long-term increases in pair density were observed in Brenne for the Pochard (Broyer 2019), in Forez for the Mallard (this study), but both species declined in Sologne. Duckling loss between the first and the third week after hatch was constant in each region for both Mallard and Pochard over the study period, but in contrast to Pochard (whose brood sizes at

Table 2. Mean (\pm s.d.) brood sizes, brood:pair ratios and pair density (pair number divided by the square root of pond surface area) for Mallard in different study areas during the first five years and the last five years of the study in each region.

Variable	Region	First 5 years	Last 5 years
Brood size	Dombes	7.92 \pm 0.71	7.80 \pm 0.68
	Forez	8.96 \pm 0.54	7.80 \pm 0.58
	Brenne	6.28 \pm 0.34	6.50 \pm 0.72
	Sologne	7.20 \pm 0.19	6.92 \pm 0.99
Brood:pair ratio	Dombes	0.43 \pm 0.06	0.21 \pm 0.13
	Forez	0.59 \pm 0.04	0.54 \pm 0.18
	Brenne	0.80 \pm 0.12	0.44 \pm 0.13
	Sologne	0.80 \pm 0.12	0.32 \pm 0.12
Pair density	Dombes	0.85 \pm 0.19	0.89 \pm 0.14
	Forez	0.61 \pm 0.19	0.97 \pm 0.22
	Brenne	1.41 \pm 0.14	1.29 \pm 0.26
	Sologne	1.58 \pm 0.45	1.22 \pm 0.28

≤ 1 week old declined), there was no significant trend in Mallard brood size (except for Forez where brood size declined). Overall, however, both species showed large-scale decreases in brood:pair ratio (except for Forez in Mallard). Thus, whereas Pochard brood:pair ratios *and* brood size systematically decreased in each region, this study reports for the Mallard a regional decreasing trend either in the brood:pair ratio (Dombes, Brenne, Sologne) or in the brood size (Forez). For a given number of Pochard pairs, the corresponding number of observed broods decreased by 33–42% throughout the study period, and one-week-old broods lost 0.5 to 1.3 chick on

average (Broyer 2019). Over the same period, Mallard brood:pair ratio declined by 40–55% in Dombes, Brenne and Sologne and brood size was lower by 1.2 chick in Forez. The extensive literature on habitat characteristics likely to affect Mallard nesting success may help us to understand what is going on in French fishponds, and these may also be affecting the Pochard nesting at these sites. In this context, two hypotheses are considered: Coypu's impact on nesting cover and fish farming recession.

Coypu became abundant in all studied regions throughout the 1990s. Bertolino *et al.* (2015) reported damages by this mammal to natural vegetation in Italian wetlands. The

extent of its negative impact on helophyte belts was studied in Dombes and Sologne and illustrated by the spectacular recovery of aquatic plants within enclosures built along unvegetated pond shores (Fig. 5). The transformation of large reedbeds into scant, linear, thinly vegetated areas certainly increased waterfowl nest concentration within the reduced available patches. Could nest predation rates be elevated as a result? Density-dependent predation rates on Mallard nests have been reported in many studies (Hill 1984; Elmberg 2003; Stephens 2003; Gunnarsson & Elmberg 2008; Elmberg *et al.* 2009), but this was not

supported by others (Ackerman *et al.* 2004; Jimenez *et al.* 2007; Padyšáková *et al.* 2010; Ringelman *et al.* 2011). Rather, Koford *et al.* (2016) pointed out that the risk posed to Mallard came from nesting in linear habitats, showing that the perimeter-to-area ratio of the vegetation patch used for nesting was the best predictor of daily nest survival. Large-scaled thinning of emergent vegetation (the usual nesting site of duck species) due to consumption by Coypu may have adversely affected Mallard nest success, potentially explaining observed decreases in the brood:pair ratio in the Mallard and, potentially for similar reasons, in the



Figure 5. Photograph showing the recovery of vegetation within an enclosure protected from the impact of Coypu grazing: taken at a demonstration meeting for pond managers in Sologne, France. Photograph by J. Broyer.

Pochard as well. Coypu may also destroy waterbird eggs directly, by using their nests as resting platforms (Bertolino *et al.* 2011; Angelici *et al.* 2012).

Fish farming abandonment was cited as one of the possible causes of Pochard population decline in Europe (Fox *et al.* 2016). Helophyte belt encroachment by woody vegetation commonly follows the cessation of management by fish farmers in Sologne, but Mallard nest survival is not necessarily lower in such conditions (Thompson *et al.* 2012), since the species may prefer to nest in shrub cover over grass (Greenwood *et al.* 1995). According to Garrick (2015), Mallard duckling survival may be adversely affected by the presence of dense nesting cover, potentially attracting predators. However, there was no such change in Sologne. Furthermore, Mallard and also Pochard brood:pair ratios decreased in Brenne and Dombes where large-scale fish farming was not abandoned, providing little evidence for a causal effect. In Forez however, Mallard brood sizes decreased after the massive demise in fish farming during the 1990s, so as to be now similar to brood sizes usually recorded in Sologne, where fish farming had declined earlier (Fig. 3). Pochard brood sizes in Brenne tended to increase with fish biomass density up to 300 kg/ha (Broyer & Bourguemestre 2020). There is therefore some evidence that habitat conditions in fishponds associated with moderately high fish productivity may also provide favourable conditions for greater duck brood sizes.

In summary, the study supports the suggestion that the impact of foraging by Coypu in reducing emergent vegetation

cover has had an adverse effect on duck nesting success in French fishponds, whereas the general decline in fish farming could be detrimental to their brood sizes. Despite this, the densities of pairs settling to breed seem to vary according to local conditions. We urge more detailed study on the effects of habitat variables (including the extent of emergent aquatic vegetation) on duck nesting success, combined with concrete experiments aiming at reducing the effect of Coypu grazing on vegetation around the fishponds. A better understanding is also required of those fish farming activities that may favour or conversely hamper brood production amongst waterfowl populations.

Acknowledgements

The author thanks the numerous fieldworkers, under the coordination of Gilles Chavas in Forez, Maurice Benmergui and Romain Chazal in Dombes, François Bourguemestre in Brenne, Luc Barbier and Sylvain Richier in Sologne.

References

- Ackerman, J.T., Blackmer, A.L. & Eady, J.McA. 2004. Is predation on waterfowl nests density dependent? – tests at three spatial scales. *Oikos* 107: 128–140.
- Angelici, C., Battisti, C., Marini, F. & Bertolino, S. 2012. Cumulative impacts of rats and coypu on nesting waterbirds: first evidence from a small Mediterranean wetland (Central Italy). *Vie et Milieu* 62: 137–141.
- Bertolino, S., Angelici, C., Monaco, E., Monaco, A. & Capizzi, D. 2011. Interactions between Coypu (*Myocastor coypus*) and bird nests in three mediterranean wetlands of central Italy. *Hystrix* 22: 333–339.

- Bertolino, S., Colangelo, P., Mori, E. & Capizzi, D. 2015. Good for management, not for conservation: an overview of research, conservation and management of Italian small mammals. *Hystrix* 26: 25–35.
- Broyer, J. 2000. La Dombes, espace d'équilibre ou simple substrat pour la culture céréalière. *Courrier de l'Environnement de l'INRA* 40: 63–65.
- Broyer, J. 2009. Compared distribution within a disturbed fishpond ecosystem of breeding ducks and bird species indicators of habitat quality. *Journal of Ornithology* 150: 761–768.
- Broyer, J. 2019. Recent changes in pair abundance and breeding results in the main French populations of the Common Pochard *Aythya ferina*. *Wildfowl* 69: 176–187.
- Broyer, J. & Bourguemestre, F. 2020. Common Pochard *Aythya ferina* breeding density and fishpond management in central France. *Wildlife Biology* doi:10.2981/wlb.00592.
- Curtet, L., Benmergui, M. & Broyer, J. 2008. Le dispositif “exclos/témoin”, un outil pour évaluer l'efficacité de la régulation du ragondin. *Faune Sauvage* 280: 16–23.
- Elmberg, J. 2003. Density-dependent breeding success in Mallard *Anas platyrhynchos* on a eutrophic lake. *Wildlife Biology* 9: 67–73.
- Elmberg, J., Folkesson, K., Guillemain, M. & Gunnarsson, G. 2009. Putting density dependence in perspective: nest density, nesting phenology and biome, all matter to survival of Mallard *Anas platyrhynchos* simulated nests. *Journal of Avian Biology* 40: 317–326.
- Folliot, B. 2018. Dynamique des espèces exploitées: le cas du fuligule milouin *Aythya ferina* dans le Paléarctique. Ph.D. thesis, CNRS-CEFE, University of Montpellier, France.
- Formosof, A.N. 1934. The Lake region of the forest steppe of Western Siberia, as a breeding area of waterfowl. *Bulletin of Moscow Society of Naturalists* 43: 256–286.
- Fournier, J.Y. & Cordonnier, P. 1982. Critères de détermination de l'âge du Canard colvert de la naissance à 9 semaines. *ONC Monthly Bulletin* No. 63 (Technical Notes, Sheet No. 10). Office National de la Chasse, Paris, France.
- Fox, A.D., Caizergues, A., Banik, M.V., Devos, K., Dvorak, M., Ellermaa, M., Folliot, B., Green, A.J., Grüneberg, G., Guillemain, M., Håland, A., Hornman, M., Keller, V., Koshelev, A.I., Kostushyn, V.A., Kozulin, A., Ławicki, Ł., Luigujõe, L., Müller, C., Musil, P., Musilová, Z., Nilsson, L., Mischenko, A., Pöysä, H., Ščiban, M., Sjenčić, J., Střpniece, A., Švažas, S. & Wahl, J. 2016. Recent changes in the abundance of Common Pochard *Aythya ferina* breeding in Europe. *Wildfowl* 66: 22–40.
- Garrick, E. 2015. Duckling survival and habitat selection of brood-rearing Mallard (*Anas platyrhynchos*) females in Southland, New Zealand. Ph.D. thesis, University of Otago, Dunedin, New Zealand.
- Greenwood, R.J., Sargeant, A.B., Johnson, D.H., Cowardin, L.M. & Shaffer, T.L. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildlife Monographs* 128: 1–57.
- Guillemain, M., Aubry, B., Folliot, B. & Caizergues, A. 2017. Estimations des tableaux de chasse de canards en France pour les saisons 2013–2014. *Faune Sauvage* 314: 22–28.
- Gunnarsson, G. & Elmberg, J. 2008. Density dependent nest predation – an experiment with simulated Mallard nests in contrasting landscapes. *Ibis* 150: 259–269.
- Hill, D. 1984. Clutch predation in relation to nest density in Mallard and Tufted Duck. *Wildfowl* 35: 151–156.
- Jimenez, J.E., Conover, M.R., Dueser, R.D. & Messmer, T.A. 2007. Influence of habitat patch characteristics on the success of upland

- duck nests. *Human-Wildlife Conflicts* 1: 244–256.
- Kalela, O. 1940. Zur Frage der neuzeitlichen Anreicherung der Brutvogelfauna in Fennoskandien mit besonderer Berücksichtigung der Austrocknung in den früheren Wohngebieten der Arten. *Ornis Fennica* 17: 41–59.
- Kalela, O. 1949. Changes in geographic ranges in the avifauna of northern and central Europe in relation to recent changes in climate. *Bird Banding* 20: 77–103.
- Koford, R.R., Dodici, G., Zenner, G., Vogel, J.A., Ness, B. & Klaver, R.W. 2016. Influence of patch shape on Mallard nest survival in Northern Iowa. *Wildlife Society Bulletin* 40: 714–721.
- Padyšáková, E., Šálek, M., Polednik, L., Sedláček, F. & Albrecht, T. 2010. Predation on simulated duck nests in relation to nest density and landscape structure. *Wildlife Research* 37: 597–603.
- Ringelman, K.M., Eadie J.M. & Ackerman, J.T. 2011. Density-dependent nest predation in waterfowl: the relative importance of nest density versus nest dispersion. *Oecologia* 169: 695–702.
- Rotella, J.J., Devries, J.H. & Howerter, D.W. 1995. Evaluation of methods for estimating density of breeding female mallards. *Journal of Field Ornithology* 66: 391–399.
- Stephens, S.E. 2003. The influence of landscape characteristics on duck nesting success in the Missouri Coteau region of North Dakota. Ph.D. thesis, Montana State University, USA
- Thompson, S.J., Arnold, T.W. & Vacek, S. 2012. Impact of encroaching woody vegetation on nest success of upland nesting waterfowl. *Journal of Wildlife Management* 76: 1635–1642.
- Tournier, H. 1990. Dynamique des populations de canard colvert et fuligule milouin en Dombes et Forez. *Alanda* 48: 58–77. [In French with English summary.]



Photograph: Male Mallard in flight, by M. Benmergui.