



## Robust estimation of survival and contribution of captive-bred Mallards *Anas platyrhynchos* to a wild population in a large-scale release programme

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The survival of captive-bred individuals from release into the wild to their first breeding season is crucial to assess the success of reintroduction or translocation programmes, and to assess their potential impact of wild populations. However, assessing the survival of captive-bred individuals following their release is often complicated by immediate dispersal once in the wild. Here, we apply Lindberg's robust design model, a method that incorporates emigration from the study site, to obtain true estimates of survival of captive-bred Mallards *Anas platyrhynchos*, a common duck species released on a large scale in Europe since the 1970s. Overall survival rate from release in July until the onset of the next breeding season in April was low ( $0.18 \pm 0.07$  se) and equivalent to half the first-year survival of local wild Mallards. Higher overall detectability and temporary emigration during the hunting period revealed movements in response to hunting pressure. Such low survival of released Mallards during their first year may help prevent large-scale genetic mixing with the wild population. Nevertheless, by combining our results with regional waterfowl counts, we estimated that a minimum of 34% of the Mallards in the region were of captive origin at the onset of the breeding season. Although most released birds quickly die, restocking for hunting may be of sufficient magnitude to affect the wild population through genetic homogenization or loss of local adaptation. Robust design protocols allow for the estimation of true survival estimates by controlling for permanent and temporary emigration and may require only a moderate increase in fieldwork effort.

**Keywords:** *Anas platyrhynchos*, hand-reared birds, hunting, reintroduction, restocking, survival.

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Monitoring the survival of captive-bred individuals from release into the wild to their first breeding season is crucial to assessing the success of reintroduction or other translocation programmes (*sensu* IUCN Species Survival Commission 2013), as well as the impact of introduced alien populations (Champagnon *et al.* 2012a). In the context of conservation translocation, accurate survival estimates allow an estimation of the 'cost of release', the greater initial mortality due to the inexperience of captive-bred individuals facing a new environment (Armstrong & Seddon 2008, Tavecchia *et al.* 2009). In the context of alien populations, assessing the contribution of exogenous individuals escaped from captivity or released intentionally for hunting or fishing is required either to rule out any risk of environmental impact or, conversely, to raise concern about the potential rapid demographic growth of the population concerned (Laikre *et al.* 2010, Champagnon *et al.* 2012a).

Accurate estimates of the survival of captive-bred individuals from release to reproduction are complicated by the immediate dispersal of individuals after release (e.g. Skjelseth *et al.* 2007). This is especially true for mobile organisms such as birds that are generally less successful in establishing self-sustaining populations after translocation (Wolf *et al.* 1996). Common capture-mark-recapture (CMR) models represent adequate tools to estimate apparent survival. However, they generally fail to estimate true survival because individuals that disperse from the study site are confounded with dead individuals (Lebreton *et al.* 1992, Lindberg *et al.* 2001, Blums *et al.* 2002). Several methodological approaches have been proposed to address this problem (Pollock 1982, Kendall *et al.* 1997, Lindberg *et al.* 2001, Schaub *et al.* 2004). Advanced CMR models such as robust design procedures are considered the most appropriate to deal with emigration and properly to estimate true survival (Sandercock 2006). Nevertheless, to our knowledge, robust design procedures have not hitherto been applied in the context of wildlife translocations.

Survival of individuals from harvested bird populations is generally assessed using data from the recovery of ringed individuals. However, parameter redundancy issues arise with ring-recovery models (see Cole *et al.* 2012 for a review). Furthermore, in most cases the estimation of monthly survival is impossible before the opening of the hunting season. Obtaining auxiliary data generally

involves using additional marks (e.g. nasal saddles in ducks) that enhance the likelihood of resightings of marked individuals that are essential for the estimation of joint models (Burnham 1993, Barker 1997, Lindberg *et al.* 2001).

Captive-bred Mallards *Anas platyrhynchos* are released in large numbers for hunting purposes in Europe. Although Mallards are released for the same purpose in North America, the magnitude of their release is currently on a completely different scale on the two continents: while fewer than 300 000 Mallards are released in North America annually into an estimated wild population of 9.2 million individuals (USFWS 2011, 2013), more than 3 million Mallards are released annually in Europe to complement an estimated wild population of 4.5 million breeding pairs (Birdlife International 2004, Champagnon 2011).

Recent studies have suggested that large-scale releases of captive-bred individuals are detrimental to the wild European Mallard population (Čížková *et al.* 2012, Vittecoq *et al.* 2012, Champagnon *et al.* 2013). Nevertheless, how many captive-bred Mallards survive the hunting season and potentially mix and breed with conspecifics is still open to question in Europe, although some information is available from North American studies (Soutiere 1989, Batt & Nelson 1990, Yerkes & Bluhm 1998, Osborne *et al.* 2010).

Our aim was to obtain robust estimates of survival for captive-bred Mallards released as juveniles to sustain local waterfowl hunting, controlling for temporal and permanent emigration to estimate the number of captive-bred Mallard that could potentially breed in the wild in the year following release. We combined data from live and dead birds in Lindberg's robust design approach (Lindberg *et al.* 2001) to estimate both monthly survival and temporary emigration rates of captive-bred Mallards fitted with nasal saddles (Fig. S1) before, during and after the hunting season. Due to the poor ability of captive-bred birds to live in the wild (Champagnon *et al.* 2012b), survival rates are expected to be lower in released birds than wild birds. Hunting, as a major source of disturbance for birds (Béchet *et al.* 2004), is likely to result in lower resighting rates during the hunting season (greater emigration; Legagneux *et al.* 2009). However, the low dispersal ability of captive-bred Mallards is likely to mitigate the magnitude of such a disturbance effect and subsequent movements by the birds.

## METHODS

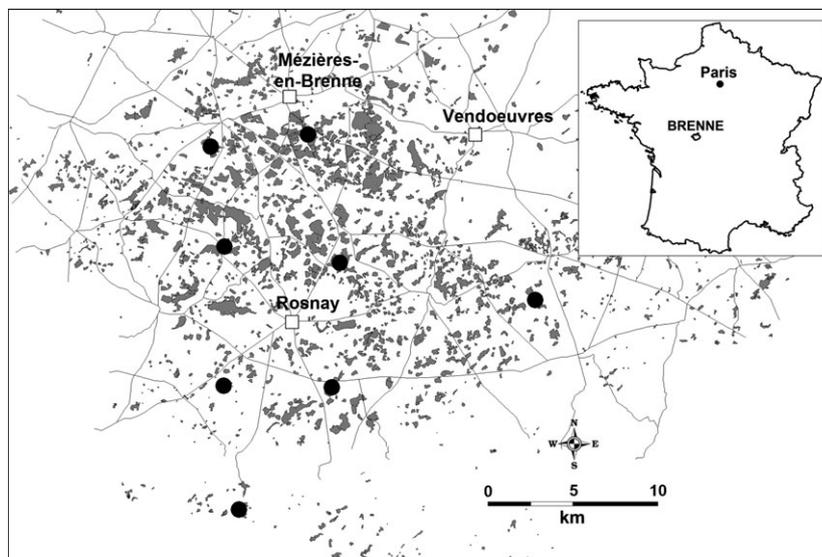
The study was conducted in Brenne, central France (46°46'N, 01°10'E), an 80 000-ha area largely devoted to fish farming and duck hunting. The area is covered with forest, wet meadows and a dispersed network of more than 2000 lakes (Fig. 1). About 48 000 Mallards are harvested annually in Brenne (F. Bourguemestre unpubl. data). This large annual Mallard harvest is made possible by the release of approximately 30 000 individuals each summer before the hunting season (F. Bourguemestre unpubl. data).

In July 2009, we experimentally released 247 female Mallard bred at a local hunting farm at the age of 6–8 weeks onto eight lakes (Fig. 1). Individuals were marked with a numbered metal ring and a red nasal saddle bearing a unique code as described in Rodrigues *et al.* (2001). The nasal saddles used here have been shown to have no negative consequences on dabbling duck behaviour or body condition (Guillemain *et al.* 2007). Only females were marked and released in this study because part of our programme was also aimed at determining whether released Mallard that survive the hunting season are able to produce young in the wild (Champagnon *et al.* 2009). At all monitored lakes, and from release date to the end of the hunting season in late January, hunters pro-

vided supplementary food (consisting of 35–50 kg of wheat grain per week per lake).

Resightings occurred throughout the 8 months from August to March, following a robust design procedure relying on the division of time into primary and secondary sessions (Pollock 1982). The primary session of interest (month) consisted of three secondary sessions (days), which represented three consecutive observation days performed around the middle of each month. Each primary session was thus divided into three secondary sessions (days). For resightings, we used a 20–60× Swarovski spotting scope to search for and identify nasal saddled birds on the eight release lakes. Observations were made from hides in the middle of the week to avoid hunting days, always from the same spot at each site by the same observer (L.V.I.) and were carried out when ducks were resting (midday). In addition to these observations of live marked birds, we also received ringing recoveries of dead birds from local hunters. These ringing recoveries always occurred between primary sessions (as we avoided weekend hunting days for observations).

To address our aim of estimating true monthly survival (from the 15th of a month to the 15th of the next month) as well as temporal and permanent emigration rates, we combined observations of live and recoveries of dead birds. We used the



**Figure 1.** Map showing the Brenne lakes and the location of the eight lakes where releases of female Mallards occurred and birds were monitored monthly thereafter (filled circles).

Lindberg robust design (RD) parameterization (Lindberg *et al.* 2001) in MARK software (White & Burnham 1999). This design provided estimates of monthly survival ( $S$ ), hunting recovery ( $r$ ), fidelity ( $F$ , the inverse of permanent emigration), sighting ( $p$ , the probability that an individual is detected during a secondary session, given that it is alive, located on the lake, and has not been previously detected during the primary session) and resighting probability ( $c$ , the probability that an individual is detected during a secondary session given that it was detected earlier during the same primary session). This model also estimates availability rather than temporary emigration (Kendall *et al.* 2013). Availability is defined as the probability of an individual to be available for detection in the primary session  $t + 1$  given that it was available in the primary session  $t$  (hereafter  $a''$ ) or unavailable in primary session  $t$  (hereafter  $a'$ ). The probability of temporarily emigrating from our sample, i.e. being outside of any of the eight monitored lakes (local scale), between primary sessions (denoted  $\gamma'$  in the original robust design; Kendall *et al.* 1997) is simply the complement of  $a''$ . Among the 1237 resightings, only eight (0.65%) occurred on a lake other than the one onto which the birds were released. This suggests virtually no movement between the eight studied lakes, and thus  $a''$  and  $a'$  reflect accurate metrics of availability from and into each release lake, respectively.

To investigate variations in parameters, we built a set of models including several combinations of time periods: fully time-dependent, constant or dependent hunting. For the hunting season, the first month of hunting (from 15 August to 15 September) was separated from the other months because hunting pressure is higher at the opening of the season (Legagneux *et al.* 2009). Outside the hunting season, we also separated pre- and post-hunting periods (August vs. March–April). This is similar to the parameterization of Legagneux *et al.* (2009). Each of these combinations of time periods was applied to each parameter (survival ( $S$ ), fidelity ( $F$ ), reporting rate ( $r$ ) and availability (both  $a'$  and  $a''$ )).

Encounter–re-encounter data are typically over-dispersed compared with theoretical expectations (Burnham & Anderson 2002). This extra-binomial variation is expressed using a variance inflation factor ( $\hat{c}$ ). We estimated  $\hat{c}$  from  $\chi^2/\text{df}$ , using the goodness-of-fit test for RD models of software RDSURVIV (Kendall & Hines 1999) applied to the most gen-

eral model (time-dependent). Model selection was then based on the Akaike information criterion (AIC) corrected for over-dispersion and small sample size (QAICc, Burnham & Anderson 2002). *A posteriori* estimations of parameter values were computed using the delta method (Seber 1982). All values are given  $\pm$  standard error (se).

## RESULTS

Of the 247 released Mallard, 70% were later observed at least once, and 52.6% were shot and reported within 7 months. The goodness-of-fit test suggested a moderate over-dispersion of the data that was taken into account in model selection by using an over-dispersion factor  $\hat{c} = 1.57$ .

From the best model (Model 1 in Table 1), survival was better modelled by separating the first month of hunting (September, i.e. 15 August–15 September:  $0.47 \pm 0.07$ ) from the other hunting months ('Hunt' in Table 1:  $0.84 \pm 0.04$ ), and pooling the non-hunting months ('Others' in Table 1, which includes the pre-hunting month (August) and post-hunting months (March and April):  $0.96 \pm 0.04$ ). The overall survival rate over all three periods (i.e. 15 July–15 April) was  $0.18 \pm 0.07$ . Recovery rate ( $r$ ) was best described by calculating values for each month. Recovery rates declined over time ( $0.79 \pm 0.09$  in September,  $0.37 \pm 0.21$  in November and  $0.18 \pm 0.16$  December). Recovery rate was impossible to estimate properly in October and January, probably due to a lack of recoveries.

Sighting ( $p$ ) and resighting ( $c$ ) probabilities showed significant variation among months (Fig. 2). Mean sighting probability  $p$  was  $0.41 \pm 0.04$ . During hunting months,  $p$  was more than twice that during non-hunting months ( $0.52 \pm 0.05$  and  $0.22 \pm 0.09$ , respectively). Overall mean resighting probability  $c$  was  $0.51 \pm 0.12$ . It also differed between hunting and non-hunting months, being greater during non-hunting months ( $c = 0.43 \pm 0.09$  and  $0.61 \pm 0.11$ , respectively).

We found a high and constant fidelity throughout the study ( $F = 0.96 \pm 0.05$ ), indicating little permanent emigration outside the Brenne region. Temporary emigration increased with hunting, being  $1 - a'' = 0.08 \pm 0.12$  in August (before the hunting season),  $0.53 \pm 0.07$  during and  $0.26 \pm 0.51$  after the hunting period. A constant return rate of temporary emigrants was found ( $a' = 0.24 \pm 0.10$ ).

**Table 1.** Modelling survival ( $S$ ), recovery ( $r$ ), availability ( $a'$  and  $a''$  depending on precedent status, see Methods for details), fidelity ( $F$ ), sighting ( $p$ ) and resighting ( $c$ ) probabilities of female Mallards released with nasal saddles in Brenne, France. The most parsimonious model is shown in bold.

No.	Model	QAICc	$\Delta$ QAICc	$\omega_i$	LL	$k$	QDev
1	<b><math>S(\text{Sept Hunt Others}) F(.) r(t) a''(\text{Aug Hunt Others}) a'(. ) p(t,.) c(t,.)</math></b>	1613.0	0.0	0.3	1.0	30	1551.5
2	$S(\text{Sept Hunt Others}) F(.) r(t) a'(\text{Aug Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1615.0	2.0	0.1	0.4	31	1553.3
3	$S(\text{Sept Hunt Others}) F(.) r(t) a'(\text{Aug Hunt Others}) a'(\text{Hunt Others}) p(t,.) c(t,.)$	1615.1	2.1	0.1	0.4	31	1551.6
4	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(t) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1615.2	2.2	0.1	0.3	31	1551.6
5	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(t) a''(\text{Sept Hunt Others}) a'(\text{Hunt Others}) p(t,.) c(t,.)$	1617.2	4.2	0.0	0.1	32	1553.4
6	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(.) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1622.0	9.0	0.0	0.0	26	1556.1
7	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(t) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1622.1	9.1	0.0	0.0	27	1551.5
8	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(\text{Sept Hunt Others}) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1622.7	9.7	0.0	0.0	28	1552.1
9	$S(\text{Sept Hunt Others}) F(.) r(t) a''(t) = a'(t) p(t,.) c(t,.)$	1623.3	10.3	0.0	0.0	34	1552.0
10	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(T) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) c(t,.)$	1624.0	11.0	0.0	0.0	26	1552.2
11	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(.) a''(\text{Sept Hunt Others}) a'(t) p(t,.) c(t,.)$	1624.1	11.1	0.0	0.0	37	1551.6
12	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(.) a''(. ) a'(. ) p(t,.) c(t,.)$	1625.7	12.7	0.0	0.0	29	1553.1
13	$S(\text{Sept Hunt Others}) F(.) r(.) a''(. ) a'(. ) p(t,.) c(t,.)$	1625.9	12.9	0.0	0.0	28	1551.6
14	$S(\text{Sept Hunt Others}) F(.) r(.) a''(\text{Aug Hunt Others}) a'(. ) p(t,.) c(t,.)$	1628.5	15.5	0.0	0.0	18	1554.0
15	$S(\text{Sept Hunt Others}) F(.) r(t) a''(t) a'(t) p(t,.) c(t,.)$	1632.0	19.0	0.0	0.4	41	1554.8
16	$S(\text{Sept Hunt Others}) F(\text{Hunt Others}) r(t) a''(t) a'(t) p(t,.) c(t,.)$	1633.9	20.9	0.0	0.0	42	1553.3
17	$S(\text{Sept Hunt Others}) F(.) r(t) a''(. ) = a'(. ) p(t,.) c(t,.)$	1640.1	27.1	0.0	0.0	27	1557.3
18	$S(\text{Sept Hunt Others}) F(t) r(t) a''(t) a'(t) p(t,.) c(t,.)$	1642.9	29.9	0.0	0.0	48	1554.2
19	$S(\text{Sept Hunt Others}) F(.) r(t) a''(\text{Sept Hunt Others}) a'(. ) p(t,.) = c(t,.)$	1646.9	33.9	0.0	0.0	19	1555.2
20	$S(\text{Sept Hunt Others}) F(t) r(.) a''(t) a'(t) p(t,.) c(t,.)$	1651.4	38.4	0.0	0.0	43	1555.7
21	$S(\text{Sept Hunt Others}) F(t) r(\text{Sept Others}) a''(t) a'(t) p(t,.) c(t,.)$	1652.5	39.5	0.0	0.0	44	1552.5
22	$S(\text{Sept Hunt Others}) F(t) r(\text{Sept Hunt Others}) a''(t) a'(t) p(t,.) c(t,.)$	1655.0	42.0	0.0	0.0	45	1553.8
23	$S(\text{Sept Hunt Others}) F(t) r(\text{Hunt Others}) a''(t) a'(t) p(t,.) c(t,.)$	1657.3	44.3	0.0	0.0	44	1553.6
24	$S(t) F(t) r(t) a''(t) a'(t) p(t,.) c(t,.)$	1659.1	46.1	0.0	0.0	56	1553.2
25	$S(t) F(t) r(t) a''(t) a'(t) p(t,.) = c(t,.)$	1673.2	60.2	0.0	0.0	48	1564.7
26	$S(t) F(t) r(t) a''(t) a'(t) p(t,t) c(t,t)$	1693.5	80.5	0.0	0.0	80	1570.2
27	$S(.) F(.) r(.) a''(. ) a'(. ) p(t,.) c(t,.)$	1731.1	118.1	0.0	0.0	21	1585.9
28	$S(.) F(.) r(.) a''(. ) a'(. ) p(. ) c(. )$	1769.6	156.6	0.0	0.0	6	1586.0
29	$S(T) F(.) r(t) a''(\text{Aug Hunt Others}) a'(. ) p(t,.) c(t,.)$	1784.7	171.7	0.0	0.0	34	1590.9

Modelling started from the fully parameterized model  $S(t) F(t) a''(t) a'(t) c(t,t) p(t,t)$ , where first and second  $t$  respectively indicate month-dependent and time-dependent while  $(.)$  indicates constant parameters.  $T$  indicated a linear trend among primary sessions. Hunt indicated months with hunting (September separated from October, November, December, January, February), Sept is the first hunting month, Others indicated non-hunting month (August and March–April). For each model, we give QAICc,  $\Delta$ QAIC, QAICWeight ( $\omega_i$ ), model likelihood (LL), number of parameters ( $k$ ) and deviance (QDev).

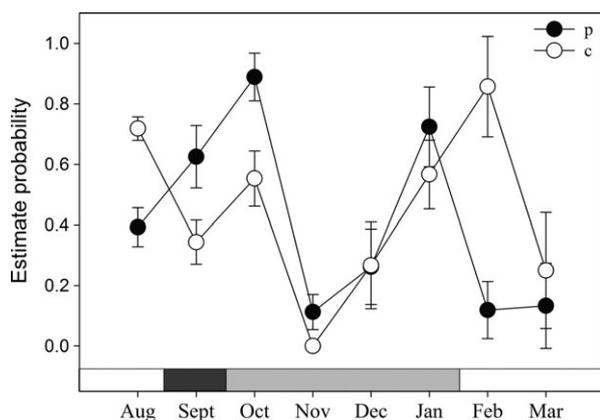
## DISCUSSION

Post-release monitoring of translocated individuals is crucial to assess the demographic consequences of management practices (IUCN Species Survival Commission 2013). In spite of their great advantages, RD models are seldom used, mostly because of logistical limitations in the field (Schaub *et al.* 2004, Sandercock 2006). These models have been applied to study breeding fidelity, philopatry and movement among moulting sites in Anatidae (Lindberg *et al.* 2001, Barker *et al.* 2005, Sedinger *et al.* 2008) or to monitor endangered long-lived species (Kendall *et al.* 2013, Peñaloza *et al.* 2014). In spite of the ability of the model to take into

account permanent and temporary emigration from the study site in the estimation of survival, to our knowledge the present study is the first to apply RD models to a wildlife translocation programme. Here, we took advantage of these model attributes to quantify the effect of hunting on post-release survival and temporary emigration.

## Survival

Survival probability from release to the onset of the next breeding season was low for captive-bred Mallards (18%) and most of the mortality occurred during the first month of hunting (the month with the greatest hunting pressure during the season;



**Figure 2.** Predicted values  $\pm$  se of the monthly probabilities of sighting ( $p$ ) and resighting ( $c$ ) of Mallard females released in Brenne in 2009. Estimates are from the best-supported model (shown in bold in Table 1). The grey bar represents the hunting period.

Legagneux *et al.* 2009). High mortality from natural causes during the first weeks following release has been reported in captive-bred ducks. For instance, Schladweiler and Tester (1972) showed that 40 of their 56 radio-marked captive-bred Mallards died within 21 days following release. Osborne *et al.* (2010) found that within a 2-month period following release, at least 60% of captive-bred Mallard died, mainly from natural causes. In our case, however, survival during non-hunting months was very high (0.96), revealing very low natural mortality, including during the first weeks after release and before the onset of the hunting season. The fact that the release lakes are managed for hunting (predator control) with important supplementary feeding (corn/wheat) may have reduced young duck mortality to a large extent after release.

Champagnon (2011) and Champagnon *et al.* (2012b) recently suggested that captive-bred Mallard released in a hunting-free area in southern France also had very low survival rates during their first year (1–16%), with a period of especially high mortality after supplementary feeding ceased (end of August). In our study, supplementary food was provided until the end of January, and no drop of survival was recorded after it ceased. Our results revealed moderately high survival for captive-bred Mallard released in central France (compared with the less than 1% survival in some study sites in southern France), but this value is nevertheless far lower than the annual survival of juvenile wild duck in Brenne ( $35\% \pm 8$  se; Champagnon J,

Legagneux P, Lebreton J-D, Gauthier-Clerc M, Bretagnolle V, Bourguemestre F & Guillemain M unpubl. data), Fennoscandinavia (21–42%; Gunnarsson *et al.* 2008) or North America (66% for immature females; Giudice 2003). Finally, our estimate did not include the breeding period, which is known to be associated with high mortality rates through predation of females on the nest (Arnold *et al.* 2012). For example, spring–summer survival rates of yearling wild Mallard females were 73% by Reynolds *et al.* (1995) and 58% by Dufour and Clark (2002). Despite dedicated habitat management, our survival estimate is thus among the lowest estimates obtained for Mallard in the wild, even for released birds (9–33% in North America; Soutiere 1989, Dunn *et al.* 1995).

### Hunting effect on movements

Our estimates of temporary emigration, sighting and resighting probabilities suggest increased mobility as a response to hunting disturbance. Higher temporary emigration during the hunting season may suggest adapted avoidance behaviour of released Mallard to hunting risk, with movements towards alternative lakes with potentially lower hunting pressure. This accords with other studies showing that hunting could alter the movement behaviour of waterfowl (Cox & Afton 1997, B chet *et al.* 2003, 2004). However, higher sighting probability and lower resighting probability during the hunting season suggest increasing movements within release lakes from one day to the next, for instance to and from open water towards reedbeds. The greater movements within the release lake during the hunting season may reflect the naive behaviour towards hunting risk of captive-bred Mallards, which may move around their release lake without finding shelter from hunting (hunting-free reserves are important refuges for wild ducks in such conditions, see Guillemain *et al.* 2008). This naive behaviour is also in accordance with a low permanent emigration from the region (4%; Legagneux *et al.* 2009). High fidelity to the lake of release and to the region where releases occur may also be explained by supplementary food resources being provided throughout the hunting season. This is also consistent with a study conducted in southern France where 92% of captive-bred Mallard recoveries were reported from the lake where birds were released (Champagnon 2011). Another study conducted in Sweden also reported lower dispersal rate of

captive-bred Mallards compared with the wild ones (Söderquist *et al.* 2013).

### Consequences of the releases for the wild Mallard population

Our results revealed that only 18% of Mallards released as juveniles in Brenne survived until the beginning of the next breeding season. Assuming that emigration of released Mallard outside Brenne is null (0.2% in Legagneux *et al.* 2009), from the 30 000 Mallards released annually, only 5300 individuals should survive the hunting season. Duck counts are carried out in mid-February in Brenne on the 300 most densely populated lakes, which represent more than 55% of the surface area covered by water. These counts provide a good estimate of the local Mallard population size (Fouque *et al.* 2004). The average from 2001 to 2010 in the Brenne area was 7480 individuals  $\pm$  414 se (Fouque C. unpubl. data). Being conservative by assuming that 50% of ducks may remain undetected during such counts (Kirby 1995), our results suggest that a minimum of 34% of the Brenne Mallards could be of captive origin at the onset of the breeding season. This estimate is almost certainly a minimum because we did not consider captive-bred Mallard that survive more than 1 year in the wild (Champagnon 2011). In addition, our estimate was based on female ducks, which generally exhibit slightly lower survival rates than males (Giudice 2003). Even if not all these birds may actually engage in reproduction, we believe that the released Mallard have a great potential for genetic introgression of the wild Brenne population (Fig. S1).

The breeding success of released Mallard could be lower than that of wild Mallard as shown from North American studies (Stanton *et al.* 1992, Dubovsky & Kaminski 1994, Osborne *et al.* 2010). In addition, Cheng *et al.* (1978) showed that captive-bred Mallard preferentially mate with a partner from the same strain, suggesting some barrier to panmixia. Finally, it has been suggested that breeding propensity of captive-bred females in the wild was lower than for their wild conspecifics, especially for first-year birds (Champagnon 2011). These results may explain why the genetic integrity of wild Mallard after 40 years of massive releases is still largely preserved in southern France (Champagnon *et al.* 2013) even if hybridization between wild and released Mallard was recently confirmed (Čížková *et al.* 2012, Champagnon *et al.* 2013).

Because captive stocks often have lower genetic diversity than wild populations (Čížková *et al.* 2012), hybridization may lead to losses of genetic diversity and disruption of local adaptations in the wild population (Allendorf *et al.* 2001). The disruptive effects of massive releases on the demographic performance of wild vertebrates have been demonstrated in other taxa. For instance, Lund *et al.* (1996) found that 20–50% of the Norwegian salmon population originated from salmon farm escapees. The breeding ability of farm-raised salmon was thought likely to threaten the native wild population (Heath *et al.* 2003) through genetic homogenization (Olden *et al.* 2004).

Whereas the early release programmes of captive-bred Mallard aimed to establish new or enhance wild breeding populations (Boyd 1957), it is now commonly accepted that low survival of captive-bred Mallards in the wild is desirable because of the limited potential adverse genetic effects on wild populations (Champagnon *et al.* 2012a). Thus, massive releases of captive-bred Mallard in Europe need to be better monitored from the conservation perspective of wild Mallard genetics. First, detailed records of Mallard releases, including the monitoring of annual numbers, should be organized by hunting agencies (Laikre *et al.* 2008). Secondly, systematic ringing of released birds should be implemented to allow the subsequent assessment of the hunted proportion of released birds, and to segregate recoveries of released birds from wild ones within ringing programmes (Champagnon 2011). We suggest individual marking (e.g. with nasal saddles) should also be promoted to allow implementation of robust demographic parameter estimations. Finally, sterilization of captive-bred individuals before their release in nature has been conducted on salmon (Cotter *et al.* 2000) and is one management action to control for the adverse genetic effects of translocations for recreational consumption, including Mallard releases (Champagnon 2011). Although feasible, Mallard sterilization would probably require surgery from veterinarians and is not likely to be a cost-effective option. To our knowledge, other alternatives to surgery, such as chemo-sterilants or immuno-contraceptives, are still not available for waterfowl and would require future research programmes.

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## REFERENCES

- Allendorf, F.W., Leary, R.F., Spruell, P. & Wenburg, J.K. 2001. The problems with hybrids: setting conservation guidelines. *Trends Ecol. Evol.* **16**: 613–622.
- Armstrong, D. & Seddon, P. 2008. Directions in reintroduction biology. *Trends Ecol. Evol.* **23**: 20–25.
- Arnold, T.W., Roche, E.A., Devries, J.H. & Howerter, D.W. 2012. Costs of reproduction in breeding female mallards: predation risk during incubation drives annual mortality. *Avian Conserv. Ecol.* **7**: 1.
- Barker, R.J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics* **53**: 666–677.
- Barker, R.J., White, G.C. & McDougall, M. 2005. Movement of Paradise Shelduck between molt sites: a joint multistate-dead recovery mark-recapture model. *J. Wildl. Manag.* **69**: 1194–1201.
- Batt, B.D.J. & Nelson, J.W. 1990. The role of hand-reared mallards in breeding waterfowl conservation. *Trans. North Am. Wildl. Nat. Resour. Conf.* **55**: 558–568.
- Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J.D. & Hines, J.E. 2003. Spring hunting changes the regional movements of migrating Greater Snow Geese. *J. Appl. Ecol.* **40**: 553–564.
- Béchet, A., Giroux, J.-F. & Gauthier, G. 2004. The effects of disturbance on behaviour, habitat use and energy of spring staging Snow Geese. *J. Appl. Ecol.* **41**: 689–700.
- Birdlife International 2004. *Birds in Europe: Population Estimates, Trends and Conservation Status*. Cambridge: Birdlife International.
- Blums, P., Nichols, J.D., Hines, J.E. & Mednis, A. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. *J. Anim. Ecol.* **71**: 438–450.
- Boyd, H. 1957. The use of hand-reared ducks for supplementing wild populations. In Scott, P. & Boyd, H. (eds). *The eighth annual report of the Wildfowl Trust 1954–1956*: 91–95. London: Country Life Limited.
- Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. In Lebreton, J.-D. & North, P.M. (eds) *Marked Individuals in the Study of Bird Population*: 199–213. Basel: Birkhäuser.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Dordrecht: Springer.
- Champagnon, J. 2011. *Conséquences des Introductions d'individus dans les populations d'oiseaux d'eau exploitées: L'exemple du canard colvert Anas platyrhynchos*. PhD dissertation, Montpellier, France.
- Champagnon, J., Guillemain, M., Gauthier-Clerc, M., Lebreton, J.-D. & Elmberg, J. 2009. Consequences of massive bird releases for hunting purposes: Mallard *Anas platyrhynchos* in the Camargue, southern France. *Wildfowl Spec. Iss.* **2**: 184–191.
- Champagnon, J., Elmberg, J., Guillemain, M., Gauthier-Clerc, M. & Lebreton, J.-D. 2012a. Conspecifics can be aliens too: a review of effects of restocking practices in vertebrates. *J. Nat. Conserv.* **20**: 231–241.
- Champagnon, J., Guillemain, M., Elmberg, J., Massez, G., Cavallo, F. & Gauthier-Clerc, M. 2012b. Low survival after release into the wild: assessing 'the burden of captivity' on Mallard physiology and behaviour. *Eur. J. Wildl. Res.* **58**: 255–267.
- Champagnon, J., Crochet, P.-A., Kreisinger, J., Čížková, D., Gauthier-Clerc, M., Massez, G., Söderquist, P., Albrecht, T. & Guillemain, M. 2013. Assessing the genetic impact of massive restocking on wild Mallard. *Anim. Conserv.* **16**: 295–305.
- Cheng, K.M., Shoffner, R.N., Phillips, R.E. & Lee, F.B. 1978. Mate preference in wild and domesticated (game-farm) Mallards (*Anas platyrhynchos*): I. Initial preference. *Anim. Behav.* **26**: 996–1003.
- Čížková, D., Javůrková, V., Champagnon, J. & Kreisinger, J. 2012. Duck's not dead: does restocking with captive bred individuals affect the genetic integrity of wild Mallard (*Anas platyrhynchos*) population? *Biol. Conserv.* **152**: 231–240.
- Cole, D.J., Morgan, B.J., Catchpole, E.A. & Hubbard, B.A. 2012. Parameter redundancy in mark-recovery models. *Biom. J.* **54**: 507–523.
- Cotter, D., O'Donovan, V., O'Maoiléidigh, N., Rogan, G., Roche, N. & Wilkins, N.P. 2000. An evaluation of the use of triploid Atlantic salmon (*Salmo salar* L.) in minimising the impact of escaped farmed salmon on wild populations. *Aquaculture* **186**: 61–75.
- Cox, R.R. Jr & Afton, A.D. 1997. Use of habitats by female northern pintails wintering in southwestern Louisiana. *J. Wildl. Manag.* **61**: 435–443.
- Dubovsky, J.A. & Kaminski, R.M. 1994. Potential reproductive consequences of winter-diet restriction in Mallards. *J. Wildl. Manag.* **58**: 780–786.
- Dufour, K.W. & Clark, R.G. 2002. Differential survival of yearling and adult female mallards and its relation to breeding habitat conditions. *Condor* **104**: 297–308.
- Dunn, J.P., Diefenbach, D.R. & Hartman, F.E. 1995. Survival and recovery distribution of wild and captive-reared Mallards. *Trans. Northeast Sect. Wildl. Soc.* **52**: 21–28.
- Fouque, C., Corda, E., Tesson, J.-L., Mondain-Monval, J.-Y., Barthe, C., Dej, F. & Birkan, M. 2004. Breeding chronology of anatids (Anatidae) and Coots (*Fulica atra*) in France. *Game Wildl. Sci.* **21**: 73–106.
- Giudice, J.H. 2003. Survival and recovery of Mallards and Gadwalls banded in eastern Washington, 1981–1998. *J. Field Ornithol.* **74**: 1–11.
- Guillemain, M., Poisbleau, M., Denonfoux, L., Lepley, M., Moreau, C., Massez, G., Leray, G., Caizergues, A., Arzel,

- C., Rodrigues, D. & Fritz, H. 2007. Multiple tests of the effect of nasal saddles on dabbling ducks: combining field and aviary approaches. *Bird Study* **54**: 35–45.
- Guillemain, M., Mondain-Monval, J.-Y., Weissenbacher, E., Brochet, A.-L. & Olivier, A. 2008. Hunting bag and distance from nearest day-roost in Camargue ducks. *Wildl. Biol.* **14**: 379–385.
- Gunnarsson, G., Elmberg, J., Dessborn, L., Jonzén, N., Pöysä, H. & Valkama, J. 2008. Survival estimates, mortality patterns, and population growth of Fennoscandian Mallards *Anas platyrhynchos*. *Ann. Zool. Fenn.* **45**: 483–495.
- Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M. & Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. *Science* **299**: 1738–1740.
- IUCN Species Survival Commission. 2013. *Guidelines for Reintroductions and Other Conservation Translocations*. IUCN/SSC.
- Kendall, W.L. & Hines, J.E. 1999. Program RDSURVIV: an estimation tool for capture-recapture data collected under Pollock's robust design. *Bird Study* **46**: S32–S38.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* **78**: 563–578.
- Kendall, W.L., Barker, R.J., White, G.C., Lindberg, M.S., Langtimm, C.A. & Peñaloza, C.L. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods Ecol. Evol.* **4**: 828–835.
- Kirby, J.S. 1995. Winter population estimates for selected waterfowl species in Britain. *Biol. Conserv.* **73**: 189–198.
- Laikre, L., Larsson, L.C., Palmé, A., Charlier, J., Josefsson, M. & Ryman, N. 2008. Potentials for monitoring gene level biodiversity: using Sweden as an example. *Biodivers. Conserv.* **17**: 893–910.
- Laikre, L., Schwartz, M.K., Waples, R.S. & Ryman, N. 2010. Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends Ecol. Evol.* **25**: 520–529.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.
- Legagneux, P., Inchausti, P., Bourguemestre, F., Latraube, F. & Bretagnolle, V. 2009. Effect of predation risk, body size, and habitat characteristics on emigration decisions in mallards. *Behav. Ecol.* **20**: 186–194.
- Lindberg, M.S., Kendall, W.L., Hines, J.E. & Anderson, M.G. 2001. Combining band recovery data and Pollock's robust design to model temporary and permanent emigration. *Biometrics* **57**: 273–281.
- Lund, R.A., Østborg, G.M. & Hansen, L.P. 1996. Escapes of farmed salmon in marine homewater and in the riverine fisheries in the period 1989–1995. *NINA Oppdragsmelding* **411**: 1–16.
- Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* **19**: 18–24.
- Osborne, C.E., Swift, B.L. & Baldassarre, G.A. 2010. Fate of captive-reared and released mallards on eastern Long Island, New York. *Hum.-Wildl. Interact.* **4**: 266–274.
- Peñaloza, C.L., Kendall, W.L. & Langtimm, C.A. 2014. Reducing bias in survival under nonrandom temporary emigration. *Ecol. Appl.* **24**: 1155–1166.
- Pollock, K.H. 1982. A capture-recapture design robust to unequal probability of capture. *J. Wildl. Manag.* **46**: 752–757.
- Reynolds, E., Blohm, J., Nichols, D. & Hines, E. 1995. Spring-summer survival rates of yearling versus adult Mallard females. *J. Wildl. Manag.* **59**: 691–696.
- Rodrigues, D.J.C., Fabião, A.M.D. & Figueiredo, M.E.M.A. 2001. The use of nasal markers for monitoring Mallard populations. In *Wildlife, Land, and People: Priorities for the 21st Century*. 316–318. Proceedings of the Second International Wildlife Management Congress. Bethesda, MD: The Wildlife Society.
- Sandercock, B.K. 2006. Estimation of demographic parameters from live-encounter data: a summary review. *J. Wildl. Manag.* **70**: 1504–1520.
- Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. 2004. Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* **85**: 2107–2113.
- Schladweiler, J.L. & Tester, J.R. 1972. Survival and behavior of hand-reared Mallards released in the wild. *J. Wildl. Manag.* **36**: 1118–1127.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance*. London: Arnold.
- Sedinger, J.S., Chelgren, N.D., Ward, D.H. & Lindberg, M.S. 2008. Fidelity and breeding probability related to population density and individual quality in Black Brent Geese *Branta bernicla nigricans*. *J. Anim. Ecol.* **77**: 702–712.
- Skjelseth, S., Ringsby, T.H., Tufto, J., Jensen, H. & Saether, B.-E. 2007. Dispersal of introduced House Sparrows *Passer domesticus*: an experiment. *Proc. R. Soc. B Biol. Sci.* **274**: 1763–1771.
- Söderquist, P., Gunnarsson, G. & Elmberg, J. 2013. Longevity and migration distance differ between wild and hand-reared Mallards *Anas platyrhynchos* in Northern Europe. *Eur. J. Wildl. Res.* **59**: 159–166.
- Soutiere, E.C. 1989. Survival rates of hand-reared Mallards released on 2 private farms. *J. Wildl. Manag.* **53**: 114.
- Stanton, J.D., Soutiere, E.C. & Lancia, R.A. 1992. Survival and reproduction of game-farm female Mallards at Remington farms, Maryland. *Wildl. Soc. Bull.* **20**: 182–188.
- Tavecchia, G., Viedma, C., Martínez-Abraín, A., Bartolomé, M.-A., Gómez, J.A. & Oro, D. 2009. Maximizing re-introduction success: assessing the immediate cost of release in a threatened waterfowl. *Biol. Conserv.* **142**: 3005–3012.
- USFWS. 2011. *Waterfowl Population Status, 2011*. Washington, DC: U.S. Department of the Interior.
- USFWS. 2013. *Review of Captive-Reared Mallard Regulations on Shooting Preserves*. Washington, DC: Division of Migratory Bird Management, U.S. Fish and Wildlife Service.
- Vittecoq, M., Grandhomme, V., Champagnon, J., Guillemain, M., Crescenzo-Chaigne, B., Renaud, F., Thomas, F., Gauthier-Clerc, M. & van der Werf, S. 2012. High influenza A virus infection rates in Mallards bred for hunting in the Camargue, South of France. *PLoS ONE* **7**: e43974.

- White, G.C. & Burnham, K.P.** 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**: S120–S139.
- Wolf, C.M., Griffith, B., Reed, C. & Temple, S.A.** 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Cons. Biol.* **10**: 1142–1154.
- Yerkes, T. & Bluhm, C.** 1998. Return rates and reproductive output of captive-reared female Mallards. *J. Wildl. Manag.* **62**: 192–198.

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## **SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Female Mallard (saddle code FNR) with 15 ducklings 1-day-old. This female was released as a juvenile in Brenne in July 2009 and photographed on 20 April 2010 in Brenne by Laura Van Ingen.