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Contribution of released captive-bred Mallards to the dynamics of the natural population

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The consequences of releasing captive-bred game animals into the wild have received little attention, despite their potential demographic impact, as well as costs and/or benefits for recipient populations. If restocking aims at increasing harvest opportunities, increased hunting pressure is expected, which would then be supported by either wild or released individuals. On the other hand, the wild recipient population may benefit from the release of captive-bred conspecifics if this reduces hunting pressure on the former through dilution of risk or selective harvesting of captive-bred individuals. Here, we modelled a Mallard (*Anas platyrhynchos*) population consisting of wild individuals supplemented by captive-bred conspecifics, a very common practice in Europe over the last 40 years. The objective was to test the effect of an increase of harvest rate on released and wild individuals, respectively. Our results show that, due to the low reproductive value of the released Mallards, the population was hardly affected by a change in harvest of these low performance individuals. Conversely, a 15 percent increase in harvest rate of the wild individuals would lead to a quick decline of the population. We discuss these results in the context of the Camargue population, located in the South of France, which has experienced an increase in Mallard harvest without apparent reduction of population size. We suggest that this has only been possible due to the release of captive-bred Mallards.

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1. Introduction

Captive-bred Mallard (*Anas platyrhynchos*) are released for hunting in at least 11 European countries (in decreasing order of importance: France, Denmark, United Kingdom, Czech Republic, Sweden, Spain, Portugal, Germany, Italy, Finland and Latvia), sometimes at a very large scale as in France, where approximately 1.4 million Mallards are released each year (Mondain-Monval & Girard 2000, Champagnon 2011). Globally, more than 3 million Mallards are estimated to be released annually in Europe compared to an estimated population of 4.5 million pairs (BirdLife International 2004, Champagnon 2011). Restocking the Mallard population aims at increasing harvest opportunities more than increasing wild population size (Fog 1971). For this purpose, captive-bred juvenile Mallards aged 3 to 12 weeks are released before the onset of the hunting season that occurs at the end of summer (third week-end of August in France; Champagnon 2011).

The contribution of captive-bred individuals to the recipient wild population depends on their individual ability to survive and breed (Fisher 1930). Recent studies conducted on more than 10,000 Mallards ringed in Sweden and France showed a similar pattern for both countries, with approximately 25% of released Mallards being shot at their release area (with a large variation among sites likely due to a variable reporting rate by hunters; Legagneux *et al.* 2009, Champagnon 2011, Söderquist 2015). From the same ringing dataset, capture-recovery model estimates suggested that survival of released birds is low during their first year, even in the absence of hunting (0.01–0.18; Champagnon 2011, Champagnon *et al.* 2012a). Nevertheless, in spite of this low survival, it has been shown in Southern and Central France that the number of released Mallards is so large that they still represent a minimum of respectively 25 and 34% of the potential breeding Mallards counted in February, i.e., at the onset of the breeding season (Champagnon *et al.* 2016).

If the reproductive value of the released Mallards is not null, then wild populations would receive a demographic support through the releases, at least in the absence of density dependence or competition processes (Champagnon *et al.* 2012b). In addition, wild recipient populations may benefit from the release of captive-bred conspecifics if the latter reduces hunting pressure on the former. Nevertheless, restocking may also increase the general interest of hunters for this species as a whole. This would result in a higher hunting pressure on both the individuals of wild as well as introduced origins, with unknown demographic consequences for the mixed Mallard population.

Evaluating the contribution of released individuals to the dynamics of an exploited natural Mallard population has not yet been performed except in North America, there considering "pure" wild-strain released Mallards (Batt & Nelson 1990). Here, based on the knowledge of the European system, we modelled a Mallard population composed of both captive-bred and wild individuals that differed genetically (Čížková *et al.* 2012, Champagnon *et al.* 2013). The population was thus considered as the mixing of two classes of individuals with different qualities as proposed by Lindberg *et al.* (2013) in Black Brant (*Branta bernicla nigricans*): released Mallards with a high mortality rate during their first year and a low breeding success, and wild Mallards with the opposite properties. Firstly, we assessed the relative reproductive value for each class of individuals. Secondly, we assessed the effect of a change (increase or decrease) in the respective hunting harvest rates of low (i.e., captive-bred) and high quality (i.e., wild) individuals. We predicted that increased harvest rate would rapidly affect the demography of the population if applied equally to released and wild groups, while selective harvest of released individuals could prevent population decline.

2. Materials and methods

2.1. General model

A simplified life cycle was built from a "birth-pulse" model (Caswell 2001; Fig. 1), considering two age classes: first-year ("1A") and more than one-year-old birds ("+1A"). Only females were considered because the population dynamics are generally determined by the availability of the scarcer sex (Caswell 2001). Annual survival of juvenile Mallards until the next breeding season (S_{1A}) differed from that of adults (S_{+1A}) (Reynolds *et al.* 1995, Gunnarsson *et al.* 2008). We intro-

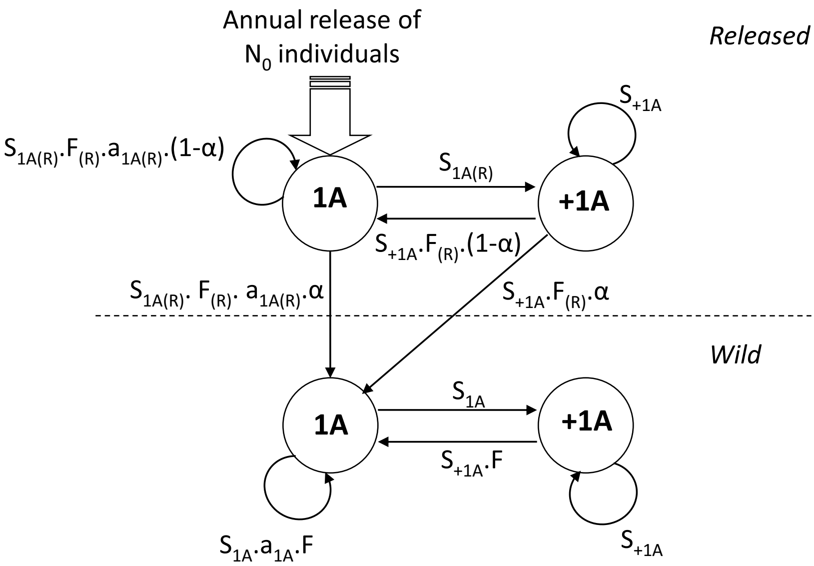

Fig. 1. Simplified life cycle for Mallards considering releases of captive-bred individuals. The description and values used for each parameter are given in Table 1.

duced a parameter to take into account the fact that not all juvenile Mallards surviving until their first breeding season attempt to breed ($a_{1A} < 1$), as opposed to older individuals ($a_{+1A} = 1$; Devries *et al.* 2008). For simplicity, we did not consider stochasticity.

2.2. Contribution of released ducks

The parameters used to run the model were of European origin whenever available (Table 1). Fecundity (F) was estimated based on an even sex-ratio at birth (Bellrose *et al.* 1961, Blums & Mednis 1996, Gunnarsson *et al.* 2008, but see Denk 2005 for the first study suggesting a male-biased ratio right from hatching) and was considered not to differ according to parental age.

The model considered a hypothetic population of 1,000 individuals with annual releases representing one-fifth of the population size. This corresponds to the known proportion of released individuals for the European Mallard population (Champagnon 2011). The annual survival rate for

Table 1. Description and value of the parameters used to model the mixed Mallard population. Subscript “(R)” stands for released. Braces stands for variation in the values depending on the scenarios (see text for details).

Group	Parameter	Symbol	Value	Source
Wild	1st year survival without hunting	S_{1A}	0.51	Corrected from Gunnarsson *et al.* (2008)
Wild	Proportion of breeders among 1st-year females	a_{1A}	0.81	Devries *et al.* (2008)
Wild	Number of fledged young females produced per pair	F	1	Gunnarsson *et al.* (2008)
Wild / Released	After 1st year annual survival without hunting	S_{+1A}	0.66	Champagnon (2011)
Released	1st year survival without hunting	$S_{1A(R)}$	0.10	Champagnon *et al.* (2012a)
Released	Proportion of breeders among 1st-year females	$a_{1A(R)}$	0.59	Champagnon (2011)
Released	Number of fledged young females produced per pair	$F_{(R)}$	0.5	Yerkes & Bluhm (1998)
Released	Proportion of wild individuals produced by released females	α	{0.8; 1}	–
Wild	Hunting harvest rate	H	0.13 ± 15%	Champagnon (2011)
Released	Hunting harvest rate	$H_{(R)}$	{0.13 ± 15%; 0.5}	Champagnon (2011)

released juvenile Mallards comes from previous studies in the south of France (Champagnon 2011). Released individuals, once adult (i.e., having survived one full hunting season), were considered as having the same survival rate as adult wild birds ($S_{+1A(R)} = S_{+1A}$). This assumption is conservative with respect to the contribution of released individuals to population growth considering that adult released birds may actually have a slightly lower annual survival than real wild ducks (Champagnon 2011).

Estimates are lacking regarding the breeding success and breeding propensity of released Mallards. As an approximation, we used the proportion of paired captive-bred females from a sample of 66 released females identified with nasal saddles from 1st March to 1st September in the Camargue in 2010 and 2011 (Champagnon 2011). Similarly, in an exploratory manner, the productivity of released females was assumed to be half that of wild females (thus 0.5 young females produced per breeding released female), following a study comparing breeding successes of released and wild pheasants (Brittas *et al.* 1992).

The performance of juvenile Mallards born in the wild from released females is probably lower than that of juvenile Mallards with wild parents, for example because of poorer maternal care in the former case (Whiting *et al.* 2010).

Factor α, which is the part of "wild" individuals produced by captive-bred Mallards, was introduced to take this into consideration. In order to evaluate sensitivity of the analysis to this parameter, we let α vary from 0.8 (only 80% of captive-bred offspring are considered of high quality, i.e., "wild") to 1 (all captive-bred offspring are considered of high quality).

Matrix models were run using Scilab (Scilab Enterprises, Versailles, France). We analysed the matrix to determine the reproductive values for each class and age, and changes in growth rate (λ) under the following harvesting scenarios.

2.3. Harvesting scenarios

We considered natural survival (S_{Nat}) values of wild Mallards and applied an effect of the proportion harvested (H) so that survival $S = S_{Nat} \times (1 - H)$ to evaluate the consequences of changing harvest on the population's demography. This equation is correct if hunting mortality occurs as a pulse, and is an approximation in other cases (Lebreton 2005). We derived the value of H following the equation $H = f / \delta$ (Anderson & Burnham 1976) where f is the ring recovery probability and δ the ring reporting probability. The ring reporting probability has never been evaluated for European hunters for any waterbird species. We hence used the value $\delta = 0.32$ estimated by (Nichols 1991) for Mallard in North America. The initial value of the proportion harvested considered was therefore $H = 0.13$ from the value of f for modern Mallards: $f = 0.04$ in Guillemain *et al.* (2015). We first applied this harvest rate to both classes, and then examined a 15% lower value, separately for each group. We then applied an extreme scenario of 0.5 harvest rate for released Mallards together with a 15% decrease in the harvested proportion of wild Mallards. The matrix model used is presented in Eq. 1.

3. Results

Assuming that all birds produced by released females are wild individuals (α = 1), the model suggested the population should decline under the current estimated harvest rate (λ = 0.983). This decline could be seen to be of limited magnitude, considering the approximation of the parameters. The reproductive value of the released juvenile Mallards was very low (3%), while that of released adults (22%) was greater, though still lower than in wild juvenile and adult Mallards (32% and 44%, respectively; Table 2).

$$\begin{bmatrix} N_{1A}(t+1) \\ N_{+1A}(t+1) \\ N_{1A(R)}(t+1) \\ N_{+1A(R)}(t+1) \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \\ N_0 \\ 0 \end{bmatrix} + \begin{bmatrix} 0.4284(1-H) & 0.658(1-H) & 0.0295\left(1-H_{(R)}\right)\alpha & 0.329(1-H)\alpha \\ 0.51(1-H) & 0.658(1-H) & 0 & 0 \\ 0 & 0 & 0.0295\left(1-H_{(R)}\right)(1-\alpha) & 0.329(1-H)(1-\alpha) \\ 0 & 0 & 0.1\left(1-H_{(R)}\right) & 0.658(1-H) \end{bmatrix} \times \begin{bmatrix} N_{1A}(t) \\ N_{+1A}(t) \\ N_{1A(R)}(t) \\ N_{+1A(R)}(t) \end{bmatrix}$$

Eq. 1. The matrix model applied for modelling population dynamics of a mixed population of Mallards (*Anas platyrhynchos*). The numbers given correspond to the group and age specific estimates from Table 1.

A decrease from 1 to 0.8 in α, the proportion of wild individuals produced by released females, had little impact on our results (Table 2). We then set α to 1 in subsequent analyses.

Given the low reproductive value of the released Mallards, the population was hardly affected by changes in survival rate of this group. This was apparent in the predicted population size for a 15% decrease in harvest of the released juvenile Mallards, from $H_{(R)}$ = 0.13 to 0.11 (Fig. 2). Conversely, the wild class was far more sensitive to changes in harvest. If harvest of wild individuals was reduced by 15% then the population increased by 0.5% each year (λ = 1.005). This pattern of an increasing population held for a harvest of released Mallards increased to *H* = 0.5 (which was a more than 3-fold increase for this class, Fig. 2 (d)).

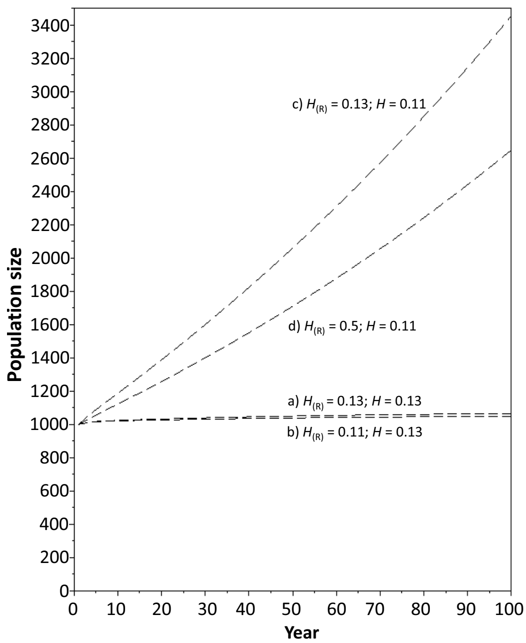

Fig. 2. Predicted population size change for 1,000 individual wild Mallards receiving 200 released birds annually under (a) best current estimates of demographic parameters, b) a 15% decrease in harvest of released birds, c) a 15% decrease in harvest of wild ducks, and d) a 15% decrease in harvest of wild ducks with an increase in harvest rate of released individuals from 0.13 to 0.5. "*H*" and "$H_{(R)}$" stands for harvest rate of wild and released Mallards, respectively.

4. Discussion

Our results showed that the released Mallards hardly contribute to the natural population, owing to their low reproductive value. They confirm the results from Batt & Nelson (1990) who found a similar pattern even though their released Mallards were of "pure" wild strain. Our results showed that the relative reproductive value of the released Mallards was 25% at its highest, and this value was almost completely supported by captive-bred Mallards that have survived at least one year. As a consequence, a modification in harvest rate of the recently released Mallards has virtually no impact on the population. In contrast, we showed that even a relatively small decrease in the harvest rate of the wild Mallards by 15% would quickly lead to a sharp population increase.

Table 2. Relative reproductive values of wild and released female Mallards. α stands for the proportion of wild individuals produced by released females.

Class	Age	Relative reproductive value	
		α = 0.8	α = 1
Wild	Juvenile	0.33	0.32
Wild	Adult	0.46	0.44
Released	Juvenile	0.02	0.03
Released	Adult	0.19	0.22

Releasing captive-bred animals into the wild is mostly practiced for birds (e.g., Willow Grouse (*Lagopus lagopus*), Houbara Bustard (*Chlamydotis undulate*), Grey Partridge (*Perdix perdix*), Red-legged Partridge (*Alectoris rufa*)) and mammals (e.g., European Rabbit (*Oryctolagus cuniculus*), Roe Deer (*Capreolus capreolus*), Red Deer (*Cervus elaphus*)) that present an economic interest. The Mallard is probably one of the few restocked species for which sufficient data are available for modelling the effect of harvest on mixed populations.

Nevertheless, this modelling exercise was limited by the availability of precise parameter estimates, so it had to be simplified with no stochastic effects, no density dependence and no uncertainty considered on the parameter estimates (Armstrong & Reynolds 2012). To include stochasticity (either environmental or demographic) would have improved the realism of our model. However, elasticity analyses provide the same results accounting or not for environmental stochasticity (Caswell 2001 Chapter 14). Regarding demographic stochasticity, this is a problem for small populations only, which is not the case of Mallards. Furthermore, it is particularly relevant to account for stochasticity when assessing probability of extinction of a population. Caswell (2001 Chapter 14) showed that elasticity in population growth rate and extinction probability are strongly correlated. Thus, our choice to build a very simple model without considering birth and survival as random events did not influence reproductive values that are estimated from a deterministic model and would not have changed the main conclusions, that the Mallard population is very resilient to the harvest of captive-bred birds compared to the harvest of wild birds.

4.1. Application to the situation in Camargue, Southern France

Although absolute figures are lacking, a long-term survey of Camargue hunting bag indices (the number of individuals harvested by hunters) from a representative sample of private hunting estates has shown that the number of Mallard harvested has significantly increased since 1992 (Mondain-Monval *et al.* 2009, J.-Y. Mondain-Monval pers. comm.). The above modelling exercise suggests that the wild Mallard population would not be sustainable without releases, given the increasing harvest rate. Despite such apparent doubling of the hunting bag, the population did not decrease but actually increased over the same period, as suggested by the positive trend of the population to which the Western Mediterranean Mallards belong (Wetlands International 2015) and the local data from Camargue (A. Tamisier, M. Gauthier-Clerc, J.-B. Mouronval, unpubl.). Together, this suggests that the observed increase of Mallard hunting bags is the result of the harvest of the ca. 50,000 captive-bred Mallards that are released annually in this region (Champagnon 2011). This is confirmed by recent genetic studies conducted in Camargue, which showed that the proportion of Mallards with a captive origin represents 75% of the total number of harvested individuals sampled ($n = 41$), whereas captive Mallards accounted for only 13% of the live birds captured in a nature reserve ($n = 39$) (Champagnon *et al.* 2013).

Higher harvest of captive-bred Mallards compared to wild ones probably results from the genuine difference in habitat selection between captive-bred and wild Mallards: wild Mallards preferentially use hunting-free areas (Guillemain *et al.* 2008) in contrast to captive-bred ones that may be more prone to hunting as they mainly stay within the most intensively hunted areas where they are released. Indeed, a recent study on mobility of captive-bred Mallards released in Brenne shows naive behaviour towards hunting risk, with the captive-bred ducks moving around their release lake without seeking shelter from hunting (Champagnon *et al.* 2016). Nevertheless, we cannot discard as an alternative explanation that this finding simply reflects higher hunting vulnerability of released Mallards compared to wild ones.

From a demographic perspective, in spite of an overall increase in the hunting pressure on Mallard, a large part of this pressure seems to be directed toward captive-bred individuals. Nevertheless, we cannot ignore that the wild population has increased to such an extent that it has supported increasing hunting pressure in Camargue for the last 20 years. Indeed a study suggests higher attractiveness of the Camargue for the short-distance migrant Teal (*Anas crecca*) consistent with habitat changes in the region (Guillemain *et al.* 2015a). Nevertheless, it seems that this situation does not apply to the Mallard, for which it has been suggested that former migrants from northern Europe have now stopped undertaking a long migration to winter quarters due to climate change (Guillemain *et al.* 2015b).

4.2. Costs and benefits of Mallard restocking

Releases of captive-bred individuals usually occur for conservation purposes (Seddon *et al.* 2012). In this context, the contribution of the released individuals is generally significant to save a species from extinction (Ebenhard 1995). For instance, restocking indeed contributed in stopping the extinction of the White Stork (*Ciconia ciconia*) in France (Massemin-Challet *et al.* 2006). Because potential survival and contribution of the released individuals to the natural population is crucial for conservation management of wild birds, adverse genetic selection in captivity is well studied and controlled as much as possible (Snyder *et al.* 1996, Robert 2009, Williams & Hoffman 2009). When population restocking is practiced for purposes of recreational or commercial harvest, it seems that released individuals are generally of poor quality in terms of reproductive value (as shown in this study, as well as in pheasants by Brittas *et al.* 1992). This is due to the low interest in counteracting genetic drift in captivity when the individuals will be released for hunting management (Champagnon *et al.* 2012a). Indeed, the aim is then to increase hunting opportunities and individuals should not necessarily survive until the next breeding season (Sokos *et al.* 2008).

Nevertheless, the hunting pressure may still deplete the wild part of the population in the presence of releases. For instance, in the case of the Red-legged Partridge, another bird species which is released on a very large scale in Europe, threats to wild individuals still exist (Bro *et al.* 2006). Indeed, these authors show that after the shooting of captive-bred individuals at the beginning of the hunting season, the pressure is then directed towards wild individuals, potentially leading to the extinction of the wild population. Furthermore, in Spain, hunting mortality was more than two-times higher in estates with restocking compared to those without (Casas *et al.* 2016). For this species, massive releases of captive-bred individuals therefore have a cost on the survival of wild individuals. We show that this scenario is unlikely in the case of the Mallard. Indeed, our study suggests that the wild part of the population may benefit from the release of Mallards, which would divert hunting pressure from the original wild birds. Nevertheless, formal assessment of the demographic effect of massive releases on wild populations should be conducted through the long-term collection of data. Genetic tools would allow estimating the proportion of the released and wild Mallards in i) hunting bags and ii) live birds captured in both hunting estates and nature reserves. By then, we would be able to estimate the hunting vulnerability of released *vs.* wild Mallards as well as potential differences in their distributions.

A central question in ecology is to understand the impact of harvesting on exploited populations. Some studies have focussed on the possible mechanisms of compensation of harvest through density-dependent mechanisms or by the selective harvest of low quality individuals (Lindberg *et al.* 2013, Péron 2013). Our study species, the Mallard, allowed us to model a population with individual heterogeneity. We show that low quality individuals (captive-bred Mallards) with low survival and breeding ability may provide a compensation mechanism for the harvest of the entire population.

Finally, captive-bred Mallards released into the wild contribute to hunting bag size, and from an economical point of view, to the general estate income for private landowners (Mathevet & Mesléard 2002, Söderquist 2015). At least in Camargue, hunters pay an annual hunting lease to the managers of private estates, the amount of such leases being positively correlated with the number of ducks available for hunting (Tamisier & Dehorter 1999: p43; Mathevet 2000: p. 258). Nevertheless, from a social perspective, hunting associated with the release of gamebirds is controversial because it is ethically questionable (Knox 2011). It is also important to highlight that from a conservation perspective, several studies have shown that hybridization with the natural population does occur, promoting genetic homogenisation even on a very large geographic scale (Olden *et al.* 2004, Čížková *et al.* 2012, Champagnon *et al.* 2013). Finally, it should be said that Mallard releases are often practiced as an easy way to obtain game for harvest, compared to more labour and cost-intensive management of wetlands to attract wild birds. The global impact of this practice for the rest of the ecosystem and for wetland biodiversity in general remains to be assessed (see e.g., Draycott *et al.* 2012), but is probably negative.

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Metsästystä varten istutettujen sinisorsien vaikutus luonnonkannan vaihteluun

Kasvatettujen riistaeläinten vapauttaminen luontoon saattaa vaikuttaa suurestikin luonnonkannan tilaan, mutta näiden toimenpiteiden seuraukset ovat puutteellisesti tunnettuja. Jos tavoitteena on lisätä metsästettävän riistan määrää, kasvanee myös metsästyspaine, joka voi kohdistua joko villeihin tai kasvatettuihin yksilöihin. Toisaalta luonnonkanta voi myös hyötyä istutuksista, koska metsästyspaine jakaantuu suuremman joukon yli, tai koska metsästys kohdistuu valikoivasti kasvatettuihin yksilöihin. Tässä työssä mallinsimme sinisorsan kantaa, joka koostuu sekä villeistä että metsästystä varten kasvatetuista ja istutetuista yksilöistä. Tämänlainen istuttaminen on ollut yleinen käytäntö Euroopassa jo viimeisen 40 vuoden ajan. Tavoitteemme oli selvittää miten metsästyspaineen kasvu vaikuttaa kasvatettuihin ja villeihin yksilöihin.

Tuloksemme osoittavat, että kasvatettujen sorsien matalan lisääntymisarvon vuoksi näihin yksilöihin kohdistuva metsästyspaineen kasvu ei juuri vaikuta kokonaiskannan kokoon. Kohdistuessaan villeihin yksilöihin, metsästyspaineen 15 prosentin kasvu johtaisi sitä vastoin kannan nopeaan vähenemiseen. Hyödynnämme tuloksia tulkitessamme eteläranskalaisen Camarguessa pesivän sinisorsakannan vaihtelua; tämä kanta on pysynyt vakaana metsästyspaineen kasvusta huolimatta, mikä on ollut mahdollista ainoastaan istutusten ansiosta.

References

Anderson, D.R. & Burnham, K.P. 1976: Population ecology of the Mallard: VI. The effect of exploitation on survival. — US Fish and Wildlife Service.

Armstrong, D.P. & Reynolds, M.H. 2012: Modelling reintroduced populations: The state of the art and future directions. — In Reintroduction biology: Integrating science and management (ed. Ewen, J.G., Armstrong, D.P., Parker, K.A. & Seddon, P.J.): 165–222. Blackwell Publishing Ltd.

Batt, B.D.J. & Nelson, J.W. 1990: The role of hand-reared mallards in breeding waterfowl conservation. — Transactions of the North American Wildlife and Natural Resources Conference 55: 558–568.

Bellrose, F.C., Scott, T.G., Hawkins, A.S. & Low, J. 1961: Sex ratios and age ratios in North American ducks. — Illinois Natural History Survey Bulletin 27: 391–474.

BirdLife International 2004: Birds in Europe: Population estimates, trends and conservation status. — BirdLife International.

Blums, P. & Mednis, A. 1996: Secondary sex ratio in Anatinae. — Auk 113: 505–511.

Brittas, R., Marcström, V., Kenward, R.E. & Karlbom, M. 1992: Survival and breeding success of reared and wild ring-necked pheasants in Sweden. — Journal of Wildlife Management 56: 368–376.

Bro, E., Mayot, P. & Mettaye, G. 2006: Opérations de repeuplement en perdrix sans arręt de la chasse : quel impact sur les populations ? Quelques éléments de réflexion sur ce mode de gestion mixte. — Faune Sauvage 274: 34–39. (In French with English summary)

Casas, F., Arroyo, B., Viñuela, J., Guzmán, J.L. & Mougeot, F. 2016: Are farm-reared red-legged partridge releases increasing hunting pressure on wild breeding partridges in central spain? — European Journal of Wildlife Research. doi:10. 1007/ s10344-015-0975-8.

Caswell, H. 2001: Matrix population models: Construction, analysis and interpretation. — 2nd Edition, Sinauer Associates.

Champagnon, J. 2011: Conséquences des introductions d'individus dans les populations d'oiseaux d'eau exploitées : L'exemple du canard colvert *Anas Platyrhynchos*. — Université Montpellier 2, PhD dissertation. (In French with English summary)

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. — Animal Conservation 16: 295–305.

Champagnon, J., Guillemain, M., Elmberg, J., Massez, G., Cavallo, F. & Gauthier-Clerc, M. 2012a: Low survival after release into the wild: assessing "the burden of captivity" on Mallard physiology and behaviour. — European Journal of Wildlife Research 58: 255–267.

Champagnon, J., Elmberg, J., Guillemain, M., Gauthier-Clerc, M. & Lebreton, J.-D. 2012b: Conspecifics can be aliens too: A review of effects of restocking practices in vertebrates. — Journal for Nature Conservation 20: 231–241.

Champagnon, J., Legagneux, P., Souchay, G., Inchausti, P., Bretagnolle, V., Bourguemestre, F., Van Ingen, L. & Guillemain, M. 2016: Robust estimation of survival and contribution of captive-bred individuals to a wild population in a large-scale release programme. — Ibis. doi: 10.1111/ibi.12341

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? — Biological Conservation 152: 231–240.

Denk, A.G. 2005: Male and female reproductive tactics in Mallards (*Anas Platyrhynchos* L.): Sperm competition and cryptic female choice. — Ludwig-Maximilian-Universität München, PhD dissertation.

Devries, J.H., Brook, R.W., Howerter, D.W. & Anderson, M.G. 2008: Effects of spring body condition and age on reproduction in Mallards (*Anas platyrhynchos*). — Auk 125: 618–628.

Draycott, R.A.H., Hoodless, A.N., Cooke, M. & Sage, R.B. 2012: The influence of pheasant releasing and associated management on farmland hedgerows and

birds in England. — European Journal of Wildlife Research 58: 227–234.
Ebenhard, T. 1995: Conservation breeding as a tool for saving animal species from extinction. — Trends in Ecology & Evolution 10: 438–443.
Fisher, R.A. 1930: The genetical theory of natural selection: A complete variorum edition. — Oxford University Press.
Guillemain, M., Pernollet, C.A., Massez, G., Cavallo, F., Simon, G. & Champagnon, J. 2015a: Disentangling the drivers of change in Common Teal migration phenology over 50 years: land use vs. climate change effects. — Journal of Ornithology 156: 647–655.
Guillemain, M., Champagnon, J., Pernollet, C.A., George, T., Momerency, A. & Simon, G. 2015b: Becoming more sedentary? Changes in recovery positions of Mallard *Anas platyrhynchos* ringed in the Camargue, France, over the last 50 years. — Wildfowl 65: 51–63.
Guillemain, M., Elmberg, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J. & Simon, G. 2010: Wintering French Mallard and Teal are heavier and in better body condition than 30 years ago: Effects of a changing environment? — AMBIO 39: 170–180.
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*. — Annales Zoologici Fennici 45: 483–495.
Knox, W.M. 2011: The antler religion. — Wildlife Society Bulletin 35: 45–48.
Lebreton, J.-D. 2005: Dynamical and statistical models for exploited populations. — Australian & New Zealand Journal of Statistics 47: 49–63.
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. — Behavioral Ecology 20: 186–194.
Lindberg, M.S., Sedinger, J.S. & Lebreton, J.-D. 2013: Individual heterogeneity in Black Brant survival and recruitment with implications for harvest dynamics. — Ecology and Evolution 3: 4045–4056.
Massemin-Challet, S., Gendner, J.-P., Samtmann, S., Pichegru, L., Wulgué, A. & Le Maho, Y. 2006: The effect of migration strategy and food availability on White Stork *Ciconia ciconia* breeding success. — Ibis 148: 503–508.
Mathevet, R. 2000: Usages des zones humides camarguaises: Enjeux et dynamique des interactions environnement-usagers-territoire. — Université Lyon 3, PhD dissertation. (In French with English summary)
Mathevet, R. & Mesléard, F. 2002: The origins and functioning of the private wildfowling lease system in a major Mediterranean wetland: the Camargue (Rhone river delta, southern France). — Land Use Policy 19: 277–286.
Mondain-Monval, J.-Y. & Girard, O. 2000: Le Canard Colvert, la Sarcelle d'Hiver et autres canards de surface. — Faune Sauvage 251: 124–139. (In French)
Mondain-Monval, J.-Y., Olivier, A. & Le Bihan, A. 2009: Recent trends in the numbers of hunters and the harvest of wildfowl in the Camargue, France: preliminary results. —Wildfowl Special Issue 2: 192–201.
Nichols, J.D. 1991: Responses of North American duck populations to exploitation. — In Bird population studies: relevance to conservation and management (ed. Perrins, C.M., Lebreton, J.D. & Hirons, G.J.M.): 498–525. Oxford University Press.
Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004: Ecological and evolutionary consequences of biotic homogenization. — Trends in Ecology & Evolution 19: 18–24.
Péron, G. 2013: Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. — Journal of Animal Ecology 82: 408–417.
Reynolds, E., Blohm, J., Nichols, D. & Hines, E. 1995: Spring-summer survival rates of yearling versus adult Mallard females. — Journal of Wildlife Management 59: 691–696.
Robert, A. 2009: Captive breeding genetics and reintroduction success. — Biological Conservation 142: 2915–2922.
Seddon, P.J., Strauss, W.M. & Innes, J. 2012: Animal translocations: What are they and why do we do them? — In Reintroduction Biology: Integrating Science and Management (ed. Ewen, J.G., Armstrong, D.P., Parker, K.A. & Seddon, P.J.): 1–32. Blackwell Publishing Ltd.
Snyder, N.F.R., Derrickson, S.R., Beissinger, S.R., Wiley, J.W., Smith, T.B., Toone, W.D. & Miller, B. 1996: Limitations of captive breeding in endangered species recovery. —Conservation Biology 10: 338–348.
Söderquist, P. 2015: Large-Scale Releases of Native Species: The Mallard as a predictive model system. — Faculty of Forest Sciences, PhD dissertation.
Sokos, C.K., Birtsas, P.K. & Tsachalidis, E.P. 2008: The aims of galliforms release and choice of techniques. — Wildlife Biology 14 : 412–422.
Tamisier, A. & Dehorter, O. 1999: Camargue, canards et foulques. — Centre Ornithologique du Gard.
Wetlands International 2015 : Waterbird population estimates. — Retrieved from wpe.wetlands.org on Wednesday 16 Dec 2015.
Williams, S.E. & Hoffman, E.A. 2009: Minimizing genetic adaptation in captive breeding programs: A review. — Biological Conservation 142: 2388–2400.
Whiting, J.C., Kelley M.S., Terry Bowyer R. & Flinders, J.T. 2010: Reintroduced bighorn sheep: Do females adjust maternal care to compensate for late-born young? — European Journal of Wildlife Research 56: 349–57.