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REPORT

Wintering French Mallard and Teal Are Heavier and in Better Body Condition than 30 Years Ago: Effects of a Changing Environment?

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Abstract Animal populations are exposed to large-scale anthropogenic impact from e.g. climate change, habitat alteration and supplemental stocking. All of these may affect body condition in wintering dabbling ducks, which in turn may affect an individual's survival and reproductive success. The aim of this study was to assess whether there have been morphometric changes in Mallard (*Anas platyrhynchos*) and Teal (*Anas crecca*) over the last 30 years at a major wintering site. Body mass and condition increased from the 1950s–1960s to the 2000s in both species. The increase in body mass amounted to as much as 11.7%, with no corresponding change in body size. Improved body condition was maintained from early to mid-winter, but then converged with historical values for late winter. Our interpretation is that increasingly benign ambient winter conditions permit ducks to maintain better energetic "safety margins" throughout winter, and that converging spring departure values may be related to evolutionary flight energetic optima. The observed changes are consistent with large-scale climate amelioration and local/regional habitat improvement (both anthropogenic).

Keywords Wing length · Body mass · Body condition · *Anas crecca* · *Anas platyrhynchos* · Climate change · Habitat change

INTRODUCTION

Wild animal populations are exposed to large-scale environmental changes due to accelerating anthropogenic impact. Long-term changes in phenology, distribution and/or morphometrics of animal populations are increasingly reported, and often attributed to global climate change (reviews in Hughes 2000; McCarthy 2001; Walther et al. 2002; Thorup et al. 2007; see also Prop et al. 1998; Thomas and Lennon 1999; Hatzofe and Yom-Tov 2002). Increase in mean body size at the population level has been demonstrated in some species (Yom-Tov and Yom-Tov 2004, 2005; Yom-Tov et al. 2008; review in Millien et al. 2006), though the opposite has also been reported (e.g. Smith et al. 1998; Yom-Tov 2001; Yom-Tov et al. 2006a). Increased body mass has been reported in wild bird populations, probably a combined effect of greater food availability and lower energy demands (e.g. Kaňuščák et al. 2004; Blackbird *Turdus merula* in Yom-Tov et al. 2006a). Other studies make no inference about growth, average size or condition at the population level, but report changed average size at some sites because the geographic range of categories of individuals differing in size had changed (e.g. Teal *Anas crecca*; Guillemain et al. 2005a). In addition to these large-scale patterns, human activities occurring at the local scale may also affect body condition and size (e.g. body size of Otters *Lutra lutra* increased in Norway in response to expanding fish farming; Yom-Tov et al. 2006b; carnivores benefiting from human garbage; Yom-Tov 2003). Agricultural practices are known to have strongly benefited some goose populations by means of improved feeding opportunities, leading to better body condition and increased abundance (e.g. Black et al. 1991). Hunted species are very likely to be affected by local management practices because the latter are often devised with the aim of attracting and/or trying to maintain local populations. In addition, supplemental stocking of farmed individuals is practiced for some game species in several countries (e.g. Laikre et al. 2006). Such releases may also contribute to observed patterns of morphometric change, having either an additive or a counteracting effect on other factors causing long-term changes in body condition or body size.

Dabbling ducks (*Anas* spp.) are among those animals in which long-term changes in body size and condition are likely to occur: many are long-distance migrants and they are often exposed to adverse winter weather (Lebreton 1973; Ridgill and Fox 1990). Dabbling ducks are also heavily hunted (e.g. 4.5 million Mallard *Anas platyrhynchos* and close to 1 million Teal shot in Western Europe annually, Hirschfeld and Heyd 2005), and in many areas hunters have a proactive attitude, managing habitats with the purpose of attracting ducks (e.g. through modification of wetlands, manipulated water levels, physical intervention into vegetation beds to promote particular plant species and seed production; Baldassarre and Bolen 2006). Lastly, release of hand-reared Mallards is a common practice in many countries (Smith and Rohwer 1997; US Fish and Wildlife Service 2003; Laikre et al. 2006), sometimes at a very large scale. In France, 1,400,000 are produced annually for hunting purposes, a number similar to the total annual bag in the country (Mondain-Monval and Girard 2000).

The aim of this paper is to assess whether dabbling duck morphometrics have changed over the long-term in a well-studied European system subjected to significant anthropogenic impact. For this purpose, we compared average body mass, wing length and body condition (body mass to wing length ratio) of ducks ringed in the Camargue, Southern France, during two time periods separated by a 30-year interval (1950s and 1960s vs. 2002–2008).

Based on previous studies, we specifically predicted that:

(1) if duck morphometrics are mostly affected by local habitat management (agriculture, management of hunting estates) making food more abundant or easier to access, or if winter climate has become more favourable, thus reducing energy requirement for wintering ducks, then both Mallard and Teal should be heavier, but not necessarily larger in the recent years compared to 30 years ago. Such local changes may not affect their growth, but would allow them putting on more fat while in the Camargue.
(2) if duck morphometrics have changed due to changes in distribution of populations at the flyway scale, then both body mass and body size should vary in the same direction within each species, but the direction may not necessarily be the same in Mallard and Teal.
(3) if duck morphometrics have changed due to releases of hand-reared birds for hunting purposes (common in recent years, almost non-existent 30 years ago), then changes towards heavier mass and larger size should be apparent in Mallard, but not in Teal, for which no releases are carried out.

METHODS

Ducks were caught in baited dabbling duck funnel traps at Tour du Valat (43°30′ N, 04°40′ E) between 14th March 1952 and 30th December 1969 (details of the Camargue technique in Bub 1991, p. 103). Ducks were sexed and aged using plumage criteria, as well as by inspection of the cloaca and the bursa of Fabricius. A total of 34,869 Teal and 6,156 Mallard were captured, ringed, sexed, aged, weighed (to the nearest g) and had their wing length measured (to the nearest mm), constituting the "historical" part of the data set (Table 1). The "modern" sample comprised 1,757 Teal and 1,371 Mallard captured with the same method, ringed and measured between 23rd October 2002 and 15th February 2008 at the Marais du Vigueirat (43°31′ N, 04°47′ E), a few kilometres from "the historical ringing site" at Tour du Valat (Table 1). Birds ringed at Tour du Valat after 1st January 1970 were not included in the analysis because some landlords and hunters started to release hand-reared Mallard and to bait the hunted areas in the Camargue in the 1970s (R. Mathevet, pers. comm.). In accordance with an earlier study (Guillemain et al. 2005a), data from the winters of 1955–1956, 1962–1963 and 1964–1965, when prolonged and serious cold spells (which likely affected general body condition in a more extreme fashion) occurred in the Camargue, were not included in the analyses, nor in the ringing totals above. No such cold spell occurred in the recent decade. Table 2 presents the means, minimum and maximum of annual means for minimum daily temperatures measured at Tour du Valat during the two time periods; although the overall means do not differ significantly between "historical" and "modern" years, winter weather nevertheless appears more benign in recent years in terms of energy expenditure since minimum annual means have been higher in early, mid- and late winter than they were 30 years ago. Throughout the paper, a "year" corresponds to a hunting/wintering season, and it is denominated by the first year of that season (e.g. 1960 for the 1960-1961 hunting season). Because relatively few birds were captured and measured in August and September, only data collected between October and March each year were considered. Dabbling duck body mass is known to fluctuate naturally through the wintering season, as bird adopt a "wintering strategy" associated with behavioural changes leading to increased body mass in mid-winter followed by a subsequent decrease of weight preceding spring departure (Tamisier et al. 1995). The comparison of "historical" and "modern" data (i.e. the two classes of the "Decade" factor) was made taking into account three modalities of the "Winter period" factor: early winter (October–November), mid-winter (December) and late winter (January–March), following Guillemain et al. (2005b). For each sex and age class in each of the two

Table 1 Number of Mallard and Teal by sex and age class measured and weighed in the Camargue, Southern France, in the 'historical' and the "modern" decades, respectively ("Decade" factor in GLMs)

	"Historical" (1952–1969)			"Modern" (2002–2008)		
	Early winter	Mid-winter	Late winter	Early winter	Mid-winter	Late winter
Mallard (*Anas platyrhynchos*)						
Adult females	103	320	428	24	64	113
Adult males	508	879	1278	60	132	321
Juvenile females	425	589	477	27	54	137
Juvenile males	444	472	233	37	105	297
Teal (*Anas crecca*)						
Adult females	313	1000	1978	91	44	113
Adult males	238	1188	4725	150	69	181
Juvenile females	2194	4083	7231	270	94	159
Juvenile males	2259	3822	5838	256	105	225

Table 2 Winter temperatures (°C) in the Camargue, Southern France, in "historical" and the "modern" decades (sampling periods), per period of the winter

	Early winter (Oct–Nov)			Mid-winter (Dec)			Late winter (Jan–March)		
	Mean	Minimum	Maximum	Mean	Minimum	Maximum	Mean	Minimum	Maximum
"Historical" (1952–1969)[a]	9.19	6.92	10.58	3.71	−0.50	4.81	4.02	1.50	7.87
"Modern" (2002–2008)	10.00	8.35	11.37	3.68	1.14	4.88	3.93	2.40	5.75
Mann–Whitney *Z*-value	−1.90 NS			0.49 NS			0.08 NS		

The three values provided per period are the mean, minimum and maximum of annual average minimum daily temperatures for each sampling period. "Historical" and "modern" values are compared for each category with the Mann–Whitney *U*-test

[a] Temperature data were only available from 1st January 1953 onwards

species, a GLM model with Decade, Winter period and their interaction as independent factors, and either body mass or wing length as the dependent variable, was first tested. Non-significant terms at $P < 0.05$ were subsequently removed when appropriate, starting with the interaction term.

In order to determine if body condition changed, the body mass:wing length ratio was computed for each individual, and the average value compared between "historical" and "modern" times (Decade factor). This analysis was performed separately for each age and sex class, but for simplicity the three periods of the winter were not separated, as this had a minor effect on body mass and wing length compared with the difference between "historical" and "modern" decades. Preliminary analyses testing the effects of both Decade and Winter period showed that the latter, despite always having a significant effect, only accounted for 9–34% of the explained variance depending on species, sex, and age classes. Although wing length is known to be affected by condition during moult, the validity of its use as a proxy for body size in Mallards as recently been demonstrated (Latorre-Margalef et al. 2009).

RESULTS

Average wing length differed between historical and modern birds in both species, and among periods of the winter in most cases, but the patterns of difference between these were inconsistent (Table 3, Fig. 1). In all cases, the difference in mean wing length between historical and modern data was very small; it ranged, all periods of the winter combined, from a 1.2% decrease in juvenile female Mallard to a 0.4% increase in juvenile male Teal.

Average body mass was consistently higher in modern than in historical birds of both species (Table 4, Fig. 2), and generally differed among periods of the winter, being the largest in mid-winter and decreasing again afterwards. In GLMs "Decade" explained much more of the variance than did "Winter period" (see relative *F* values in the models in Table 4), mainly because the difference between decades was far smaller in late winter than in early and mid-winter (Fig. 2). The average difference between historical and modern birds was nonetheless very large since it ranged, when all periods of the winter were combined, from a 7.3% increase in juvenile male Mallards to an 11.7% increase in adult female Teal.

Table 3 Results of GLMs comparing average wing length of Camargue Mallards and Teal (by sex and age class) between historical (1952–1969) and modern (2002–2008) sample periods ("Decade"), also testing for differences between periods of the winter (early: Oct–Nov; Mid-: Dec; Late: Jan–Mar; "winter period") and for the interaction between these two factors

Species	Sex/Age class	Parameter	df	F	P value
Mallard	Adult males	Complete model: $F_{3,\ 3174} = 9.18$; $P < 0.0001$			
		Winter period	2	9.07	0.0001
		Decade	1	10.05	0.0015
	Juvenile males	Complete model: $F_{3,\ 1584} = 11.57$; $P < 0.0001$			
		Winter period	2	5.95	0.0027
		Decade	1	7.10	0.0078
	Adult females	Complete model: $F_{3,\ 1048} = 7.89$; $P < 0.0001$			
		Winter period	2	4.78	0.0086
		Decade	1	14.83	0.0001
	Juvenile females	Complete model (*Decade*): $F_{1,\ 1707} = 55.24$; $P < 0.0001$			
Teal	Adult males	Complete model (*Decade*): $F_{2,\ 6548} = 0.84$; NS			
	Juvenile males	Complete model: $F_{5,\ 12499} = 12.74$; $P < 0.0001$			
		Winter period	2	0.18	NS
		Decade	1	18.29	<0.0001
		*W period*Decade*	2	4.20	0.0150
	Adult females	Complete model (*Decade*): $F_{2,\ 3536} = 11.02$; $P < 0.0001$			
	Juvenile females	Complete model: $F_{5,\ 14025} = 4.51$; $P = 0.0004$			
		Winter period	2	2.52	NS
		Decade	1	1.60	NS
		*W period*Decade*	2	3.82	0.0219

Only final models are presented (see text)

Average body condition (body mass/wing length ratio) showed a pattern over the winter similar to that of plain body mass; it was markedly lower in the historical than in the modern decade in Teal (t-tests: all $t > 14.11$, all $P < 0.0001$; Fig. 3) as well as in Mallard (t-tests: all $t > 9.82$, all $P < 0.0001$; Fig. 4).

DISCUSSION

Mallard and Teal wintering in the Camargue showed a consistent significant increase in body mass from the 1960s to the present day, whereas a corresponding change was not seen in average wing length. In other words, ducks have increased their body condition rather than become larger, as demonstrated by the changes in body condition index.

The people measuring the birds changed between the two study periods. However, an earlier analysis from the Camargue shows that the difference in mean wing length in Teal measured by different observers, for a given year and given age and sex classes, was only 0.9 mm, and in only one of 43 cases was the difference more than 2.5 mm (computed from Appendix 1 in Guillemain et al. 2005a). Differences in wing length between the two periods of the present study exceed these values, and are therefore unlikely to result merely from observer biases.

It is unlikely that the observed body mass increases were due to trapping method biases, since the same type of funnel trap was used in the Camargue at the Tour du Valat during the 1950s and 1960s and in Marais du Vigueirat in later years. Furthermore, while the area surrounding the traps was baited with grain (especially rice) at both sites (hence in both study periods), some baiting was also done inside "the historical time period" traps at Tour du Valat to feed live decoys kept inside (A.R. Johnson, pers. comm.). In contrast, rice was only placed outside the traps and in the entrance funnels at Marais du Vigueirat. It is, therefore, not possible that birds have become fatter simply because they can feed more intensively in the traps. The fact that there was food inside the traps in "historical" years but not in "modern" also allows ruling out a potential bias associated with "catch size": it is a fact that many more birds were caught in the 1950s–1960s than during the last decade, so that birds may have then spent more time in traps and ringing bags before being ringed and weighed. However, ducks were able to feed in the traps in the "historical" years while this is no longer possible, so that the differences in observed body mass may not reflect the simple fact that it took longer to ring birds during "historical" years. It is also unlikely that

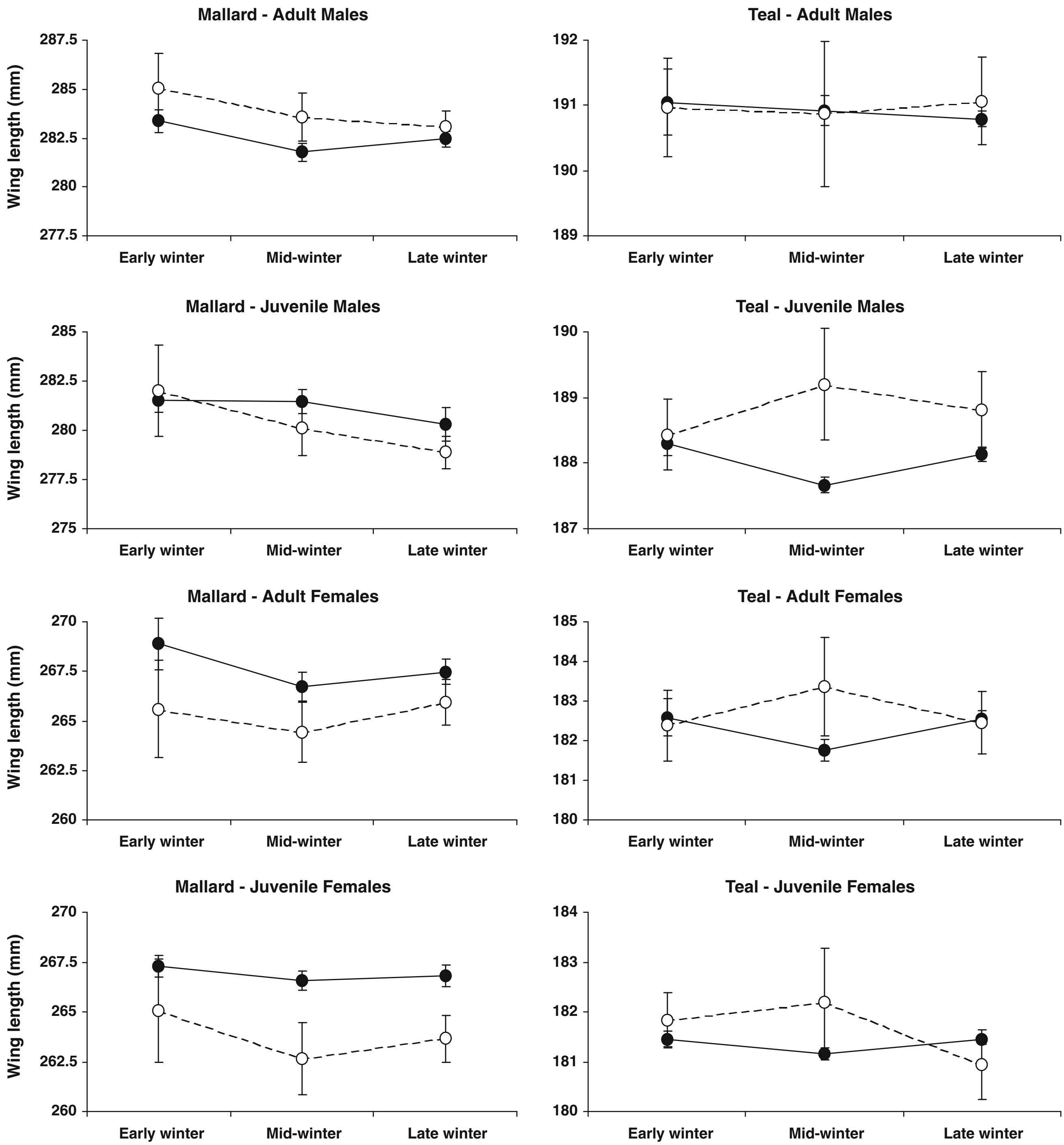

Fig. 1 Average wing length of Camargue Mallard and Teal by sex, age class, and winter period. *Closed circles* show historical data, *open circles* show modern data. See Table 1 for sample sizes per period of the winter, and Table 3 for statistics. *Vertical bars* show 95% confidence intervals

the recorded differences in average body mass reflect an observer bias: while the precise measurement of duck wing chord does require some experience (see observer differences above), no such skill is needed to weigh a bird, and the reading of this measurement is straightforward.

The intra-annual pattern observed here for both species shows that all age and sex categories start the winter with a higher body mass in recent years than before, and that this advantage remains of the same magnitude until mid-winter (Fig. 2). We argue that such increases in average body mass of Mallard and Teal are large enough to have major fitness consequences with respect to winter survival. In mid-winter, the 38–61 g increase in body mass recorded in Camargue Teal would translate, assuming its daily energy

Table 4 Results of GLMs comparing average body mass of Camargue Mallards and Teal (by sex and age class) between historical (1952–1969) and modern (2002–2008) sampling periods ("Decade"), also testing for differences between periods of the winter (Early: Oct–Nov; Mid-: Dec; Late: Jan–Mar; "Winter period") and for the interaction between these two factors

Species	Sex/Age class	Parameter	df	*F*	*P* value
Mallard	Adult males	Complete model: $F_{3,\ 3172} = 104.31$; $P < 0.0001$			
		Winter period	2	113.59	<0.0001
		Decade	1	254.89	<0.0001
		*W period*Decade*	2	13.89	<0.0001
	Juvenile males	Complete model: $F_{5,\ 1582} = 41.21$; $P < 0.0001$			
		Winter period	2	28.65	<0.0001
		Decade	1	135.86	<0.0001
		*W period*Decade*	2	21.09	<0.0001
	Adult females	Complete model: $F_{3,\ 1048} = 60.77$; $P < 0.0001$			
		Winter period	2	47.66	<0.0001
		Decade	1	96.01	<0.0001
	Juvenile females	Complete model: $F_{5,\ 1703} = 20.97$; $P < 0.0001$			
		Winter period	2	16.07	<0.0001
		Decade	1	87.90	<0.0001
		*W period*Decade*	2	9.62	0.0118
Teal	Adult males	Complete model: $F_{5,\ 6545} = 126.29$; $P < 0.0001$			
		Winter period	2	49.48	<0.0001
		Decade	1	437.80	<0.0001
		*W period*Decade*	2	34.17	<0.0001
	Juvenile males	Complete model: $F_{5,\ 12499} = 189.79$; $P < 0.0001$			
		Winter period	2	68.15	<0.0001
		Decade	1	647.59	<0.0001
		*W period*Decade*	2	71.14	<0.0001
	Adult females	Complete model: $F_{5,\ 3533} = 77.81$; $P < 0.0001$			
		Winter period	2	53.09	<0.0001
		Decade	1	242.18	<0.0001
		*W period*Decade*	2	24.34	<0.0001
	Juvenile females	Complete model: $F_{5,\ 14025} = 122.41$; $P < 0.0001$			
		Winter period	2	29.25	<0.0001
		Decade	1	288.79	<0.0001
		*W period*Decade*	2	39.90	<0.0001

Only final models are presented (see text)

need is around 100 kcal (Baldassarre et al. 1986) and 1 g of stored lipids corresponds to 9 kcal, into the ability to fast for ca. 3.5–5.5 days in case of adverse conditions (e.g. cold spell making food unavailable through the freezing of wetlands). However, it should be noted that the difference between historical and modern years when it comes to body mass is much smaller in late winter that during the earlier parts of the winter. Although measurements provided here come from different individuals within a given study season, in order to ensure statistical independence of data from the three winter study periods, previous analyses based on repeated recaptures of the same individuals nevertheless confirm that the observed pattern of body mass change is indeed a genuine individual wintering strategy (birds first gaining then losing body mass) rather than a bias caused by sampling birds from different populations during the course of the winter (Guillemain et al. 2005b). This indicates that although modern birds have better "safety margins" in terms of body condition in early and mid-winter, they nonetheless tend to converge in body mass (and body condition) with historical birds in late winter (see also Tamisier et al. 1995). We hypothesize that this reflects deeply embedded selective regimes to attain an optimal departure body mass in preparation for spring migration (e.g. Lindström and Alerstam 1992).

We here demonstrate a dramatic increase in early and mid-winter body condition in Teal and Mallard over the last 30 years. This relatively rapid change, be it

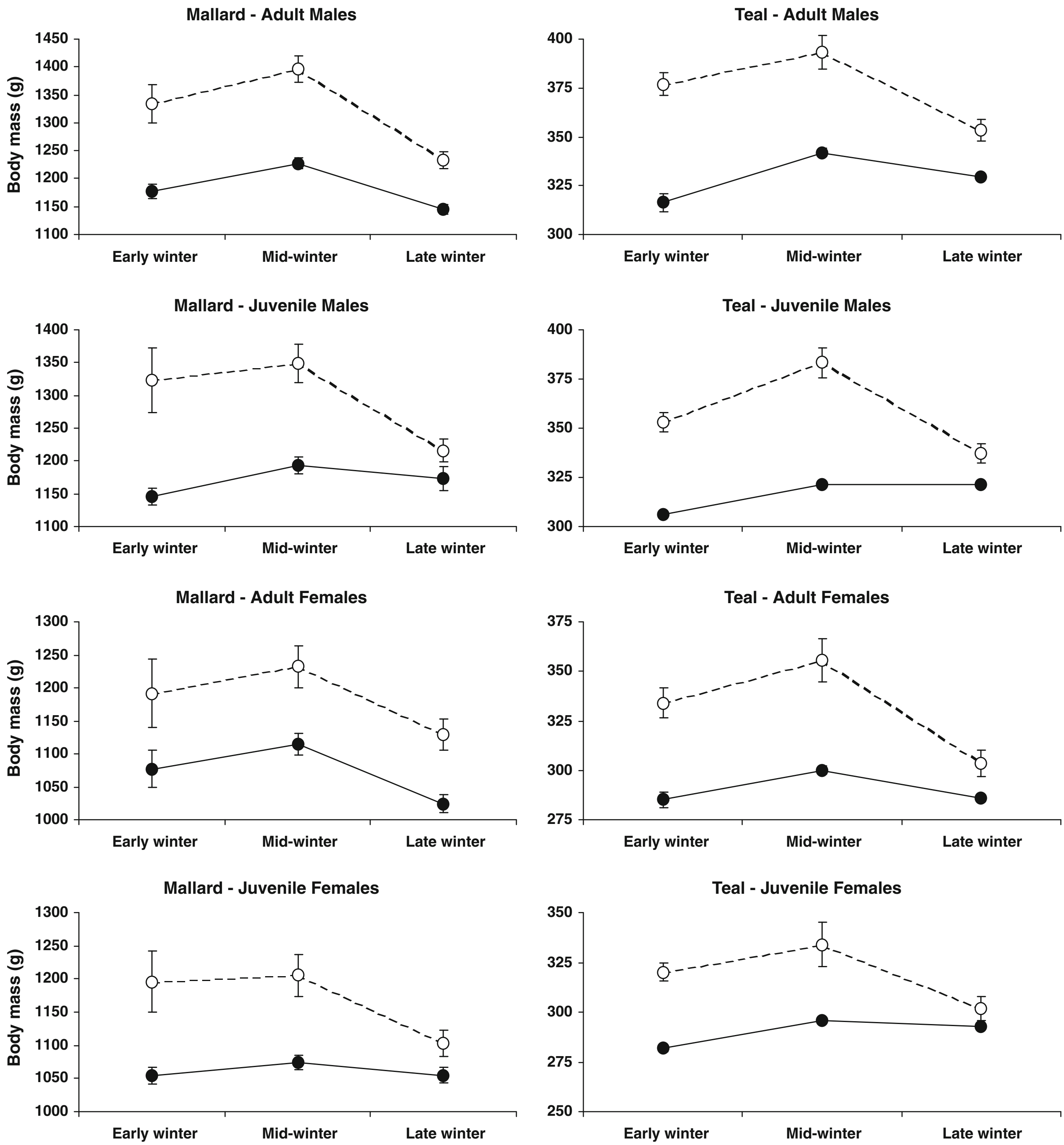

Fig. 2 Average body mass of Camargue Mallard and Teal by sex, age class, and winter period. *Closed circles* show historical data, *open circles* show modern data. See Table 1 for sample sizes per period of the winter, and Table 4 for statistics. *Vertical bars* show 95% confidence intervals

phenotypic, genotypic or both, may be addressed within the framework of at least four mutually non-exclusive hypotheses: (i) global climatic change, (ii) geographical shifts of winter range of populations, (iii) local or regional habitat improvement anywhere along the flyway, and (iv) large-scale supplemental stocking for hunting purposes. We will address each of these in turn.

The patterns of change found by us are consistent with improved wintering conditions for dabbling ducks. Such improvements may be apparent for the Camargue area through milder minimum temperatures (i.e. fewer cold years in more recent times; Table 2). While it has been shown that climate change may affect terrestrial bird populations negatively (e.g. Julliard et al. 2003), cold

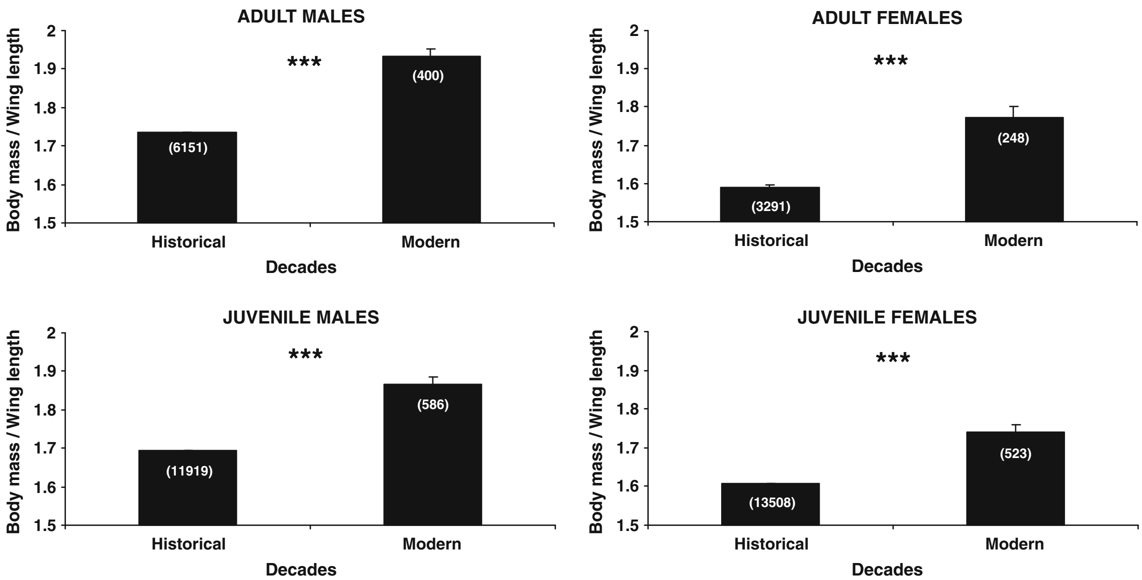

Fig. 3 Body condition index (body mass/wing length ratio) of Camargue Teal. *Vertical bars* show 95% confidence intervals, sample sizes are indicated in brackets. The stars indicate that all differences were significant at the 0.0001 level in *t*-test comparisons (see text)

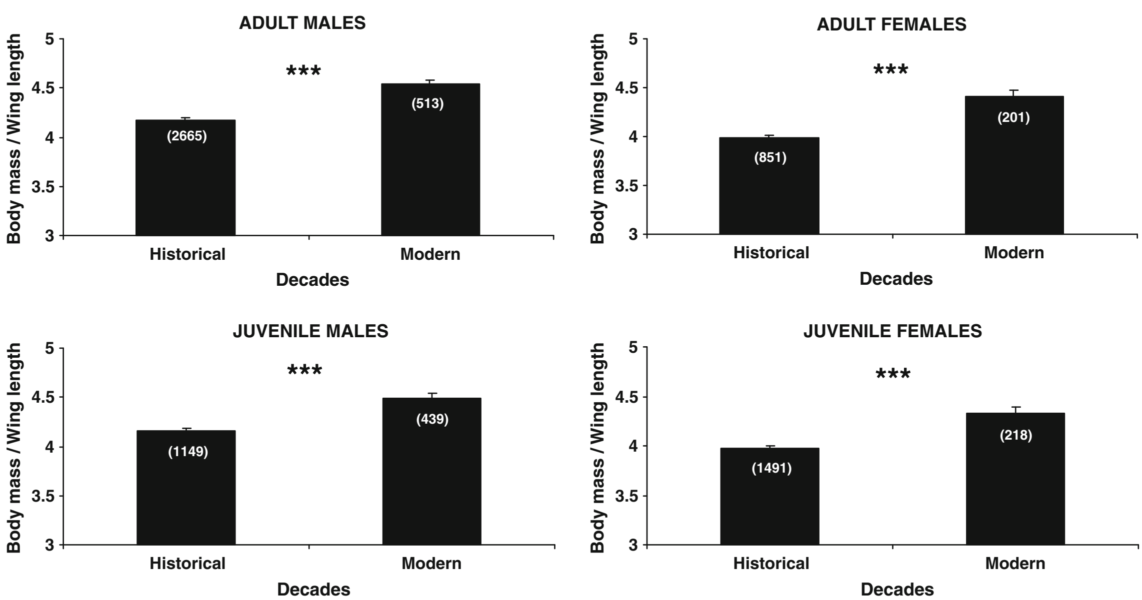

Fig. 4 Body condition index (body mass/wing length ratio) of Camargue Mallards. *Vertical bars* show 95% confidence intervals, sample sizes are indicated in brackets. The stars indicate that all differences were significant at the 0.0001 level in *t*-test comparisons (see text)

temperatures are a limiting factor for wintering waterbirds, especially for dabbling ducks, whose access to food is quickly restricted if ice forms (e.g. Ridgill and Fox 1990). Benign wintering conditions may also allow dabbling ducks to build up larger reserves because their demands for thermoregulation decrease, and/or because major food sources do not become less abundant or more restricted (e.g. continued plant growth during mid-winter, fewer and shorter periods when foraging sites freeze over). This interpretation is consistent with that of Kaňuščák et al. (2004) for River Warbler (*Locustella fluviatilis*) and of Yom-Tov et al. (2006a) for Blackbird. In this context, it is worth noting that improved body condition was also observed over the last decades for Teal wintering in Essex, UK (R. King, unpublished data) suggesting this is a large-scale change consistent with a global temperature increase.

Shifts in geographical range in response to climate change have been documented in other species (reviews in Hughes 2000; McCarthy 2001), including a number of European waterbirds. Such shifts can be hypothesized to occur in waterfowl as well (e.g. Guillemain et al. 2005a). However, we only observed a change in mass and body condition index, not in size (wing length), strongly indicating that such shifts have not taken place. Moreover, there are no indications from ringing recoveries that a shift in recruitment area has taken place in either species (ONCFS, Unpublished data available at www.oncfs.gouv.fr), i.e. it is unlikely that birds are heavier simply because they now have to travel shorter distances during migration episodes or come from milder regions, or because heavier birds that wintered further North in the past now come more markedly in the Camargue.

It is possible that local environmental conditions encountered during or even before autumn migration have improved over the last decades, so that Teal and Mallard now have larger fat stores already when they arrive at their Camargue wintering sites. One such factor might be recent improvements in the network of protected sites that these birds use as stopovers in late summer and early autumn (Madsen and Clausen 1998). Our results are consistent with this idea, but morphometric data from such sites in autumn are critically needed to test its validity. Further, it is impossible to assess for how long the birds captured and weighed in the Camargue in early winter have been there. More importantly, the fact that they maintain an improved body condition from early to mid-winter suggests that local environmental conditions in the Camargue itself have become more benign over recent decades.

Indeed, agricultural practices in general have changed in the Camargue over the last 30 years. The area cultivated for rice peaked at over 30,000 ha in 1960 and has since decreased (Mathevet 2004). Furthermore, some rice fields were regularly flooded after harvest in the past, providing valuable foraging opportunities to wintering dabbling ducks (e.g. Pirot et al. 1984). This is less frequently the case nowadays, when rice harvest is rapidly followed by ploughing of the fields, making spilt grain less available to ducks. Thus, it is unlikely that rice farming has improved environmental conditions for ducks over this period. Two other main habitat changes have occurred in recent decades, in addition to the general loss of wetlands mostly to agriculture, salt exploitation and industry (Tamisier and Grillas 1994), namely the concomitant increase of protected areas (an increase by ca. 3,000 ha since 1970, calculated after Table 4 in Tamisier and Isenmann 2004) and the intensification of wetland management practices dedicated to hunting within large private estates (Tamisier and Grillas 1994). Earlier analyses show that Camargue Teal remaining in protected areas were in better condition than those relying on surrounding hunted areas for foraging (Guillemain et al. 2007). The increase in protected area in the Camargue may in this sense have contributed to the improved body condition of dabbling ducks wintering in the entire Rhône delta (note that both trapping areas in the present study had already been protected for some time before catching of ducks started). In parallel, hunted wetlands are now increasingly artificially flooded in order to promote hydrophyte development (Tamisier and Grillas 1994), the seeds of which constitute a major food source for wintering Teal and Mallard (Tamisier and Dehorter 1999). Baiting within hunting estates is also a common practice nowadays, both here as well as in some other French wintering quarters. An analysis of Teal and Mallard diets in Brenne, western France, revealed that bait represented 65% and 45% of food dry weight in the two species, respectively (Legagneux 2007). The amount of bait spread in Camargue is unknown, and will be difficult to estimate since an unknown part of it is directly produced within some estates. Nevertheless, this amount probably increased markedly over the last 30 years, and it is a likely candidate to explain the concomitant improvement of dabbling duck body condition recorded in this study. A future detailed analysis of Mallard and Teal diets in the Camargue, allowing comparison with data from the 1970s, may help in assessing the relative potential role of baiting versus wetland modifications and climate change on dabbling duck body condition.

Another goal of this study was to assess if the relatively recent practice of releasing hand-reared Mallard for hunting affects average body size and mass. This is apparently not the case: although body mass did increase in Mallard, it also did so in Teal, a species for which releases are not practised. Alternatively, the two species might not react to the same factors, i.e. Mallard body mass may have increased because the population increasingly comprises birds of hand-reared origin, whilst Teal body mass may have increased for another reason. We find this latter scenario very unlikely, though, since Mallard and Teal have the same general habits, especially concerning foraging (both are granivorous in winter, and often rely on the same seed species within the same region whenever possible, e.g. Guillemain et al. 2002). Any improvement beneficial to Teal in terms of body mass is therefore likely to benefit Mallards, and in this case the additional effect of releases for hunting would make body mass changes in Mallard more pronounced than in Teal, which was not observed.

To conclude, our data are consistent with the hypotheses that global climate warming and local habitat management, both being anthropogenic processes, could have lead to the observed improvement in body condition in two widespread and heavily hunted waterfowl species. At the same time, other studies relying on ring recoveries found little support for the hypothesis that a shift in the geographical range of intraspecific populations occurred, and could therefore be held responsible for the observed morphometric changes. More surprisingly, though, we find no support for the hypothesis of large-scale releases of hand-reared birds. There are no data available about morphometrics of hand-reared birds used in stocking programs, but it has often been presumed that they are bigger and may thus affect the wild phenotype by gradual genetic introgression. This needs to be studied further.

Wild Teal and Mallards may seemingly benefit in the short-term from the expected fitness improvement associated with body condition increase. However, the longer-term consequences of body mass change may not be positive for these populations and their environment in general. For example, the changes in wetland management practices that are apparently beneficial to ducks may also be associated with a loss of local biodiversity in other taxa (Tamisier and Grillas 1994), requiring these processes to be monitored and studied further in the future. The present data do not allow us to distinguish between the "global change" and the "habitat improvement" hypotheses, and it is not possible to rule out that yet another factor, or combinations of factors, explain the observed patterns better still. Nevertheless, at present we interpret the observed massive morphometric changes in western European Teal and Mallards as resulting from anthropogenic causes of a rapidly changing environment.

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