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ORIGINAL ARTICLES

Long-term climatic trend and body size variation in teal *Anas crecca*

Matthieu Guillemain, Jean-Yves Mondain-Monval, Alan R. Johnson & Géraldine Simon

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A general warming of climate in the future may profoundly affect wildlife populations in terms of numbers, distribution and characteristics of the individuals, therefore leading to new challenges in terms of management and conservation. The effects of global warming can already be detected through the analysis of long-term databases, but insights into these processes can also be acquired by studying changes in wildlife populations during periods with clear trends in climatic changes. We analysed ringing data from more than 38,000 teal *Anas crecca* caught at the Station Biologique de la Tour du Valat in the Camargue, Southern France, between September 1954 and April 1971. Temperature in the Camargue clearly decreased over the ringing period. There was no correlation between average annual body mass and temperature in any age or sex class, nor a significant effect of temperature on the age ratio of the population. In adults, there were more males when average daily maximum winter temperature increased, while the opposite trend was found for juveniles. The clearest pattern we observed was a positive relationship between temperature and wing length of the individuals: in all sex and age classes, birds tended to get smaller as temperature decreased. It is unlikely that this pattern was related to harsh climate affecting teal feather growth. Rather, we hypothesise that climate affected the distribution of the individuals in Europe: as temperature got colder, small birds found it still more difficult to remain in northern areas and increasingly used the Camargue as a refuge. Reversing the observed pattern suggests that a global warming of climate in the future may have profound consequences for the distribution of wintering teal in Europe, as more and more birds will become able to remain in northern areas closer to their breeding grounds.

Key words: Anas crecca, body size, Camargue, climate change, teal

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The potential future effects of global warming increasingly concern wildlife biologists, since a general warming of the climate may profoundly affect species distribution and characteristics. Because they are highly mobile, birds, especially migratory species, are very likely to respond markedly to such general environmental changes. The analysis of historical data sets has already demonstrated changes in behaviour, distribution and even morphology of bird species over decades, which have been proposed to be a consequence of gradually increasing temperatures (e.g. Jakober & Stauber 2000, Yom-Tov 2001, see McCarty 2001 for a review).

Ducks are among the bird species that are very likely to be affected by changes in climate: most duck species have distinct breeding and wintering areas, often several thousand kilometres apart. Because of the costs associated with such long migrations, it is generally considered that individuals should try to remain as close to their breeding areas (i.e. as far north) as possible during the winter. Support to this idea is given by the general north-east/south-west gradient of age and sex ratios in wintering European duck populations: because their surface/mass ratio allows them to do so, or because they are dominant in intersexual competition, adult males are more likely to winter in the north-east, while more females and juveniles winter further south-west (e.g. Nichols & Haramis 1980, Campredon 1983, Carbone & Owen 1995, Evans & Day 2001). Within a sex and age class, similar gradients in body size have also been recorded, with larger birds in the east of Europe (e.g. Cramp & Simmons 1977). Dabbling ducks are known to be highly susceptible to cold spells, with major displacements to the south-west observed in case of very cold winters (Lebreton 1973, Ridgill & Fox 1990). It could therefore be expected that fewer birds would have to winter in the current south-west limit of their range if temperatures were to increase gradually in the future. If the hypothesis that it is the surface/mass ratio that determines where a dabbling duck can winter is true (which is likely given the east-west body size gradient described in Cramp & Simmons 1977), then a gradual change in the average morphology of birds wintering at a particular site should also be observed, as the smallest individuals should gradually become more likely to stay north in winter.

An analysis of historical duck measurement data over the last 50 or 100 years should detect such a phenomenon. Alternatively, data from shorter periods when many ducks were ringed and temperature has shown a clear trend over time (towards either an increase or a decrease) may help studying these patterns. Such a data set exists at the Station Biologique de la Tour du Valat, in the Camargue, southern France where close to 60,000 teal *Anas crecca* were ringed from the early 1950s to the late 1970s. Meanwhile, a clear trend of both average minimum and average maximum temperature decrease was observed (see below).

The aim of this study was to test if the body size of teal ringed in the Camargue indeed showed a clear pattern over this period of climatic change.

Methods

Teal were caught at the Station Biologique de la Tour du Valat, Camargue (43°30'28N, 04°40'07E), using standard dabbling duck funnel traps hidden in the vegetation (details of the Camargue technique in Bub 1991: 103). Teal wintering in the Camargue mainly breed in Fennoscandia and the former USSR. Given its position in the south of the species' range and its generally mild climate, the Camargue is used as a refuge by birds in case of cold spells in the north: the general pattern is then a major influx of northern individuals, with massive increases in bird numbers.

The same professional ringers handled and examined all the birds. Ducks were sexed and aged using plumage criteria, and inspection of the cloaca and the bursa of Fabricius. A total of 59,184 teal were captured between 1952 and 1978. Most (i.e. 97.8%) of the birds were captured between September 1954 and April 1971, and 38,416 of these were effectively sexed, aged and their wings measured to the nearest mm; these 38,416 birds constitute the sample of our study. A minimum of 58 individuals (adult females in 1954/55) were caught per winter, age and sex class (maximum 4,705 first-winter females in 1957/58; Fig. 1).

Temperature data were recorded daily between 1 December and 28 or 29 February at the Météo France station in Istres situated 22.5 km east of the ringing site

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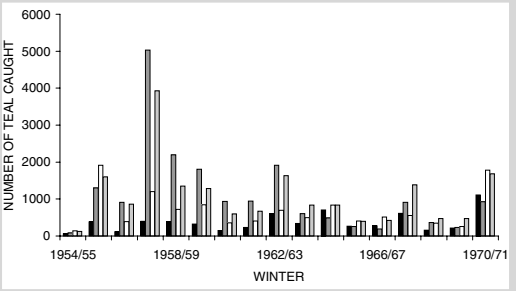


Figure 1. Number of teal caught at the Tour du Valat per winter during 1954/55-1970/71, per age and sex class for adult females (■), first-year females (■), adult males (□) and first-year males (□).

for the 1952-1961 period, and at the Station Biologique de la Tour du Valat itself for the 1962-1978 period. It is very unlikely that the switch from one station to another had a great effect on the results since, although the difference between the two stations was significant, daily maximum temperatures in December, January and February during 1962-1970 were only 0.16°C higher at Istres, whereas conversely daily minimums were 0.12°C higher at the Tour du Valat (P. Chauvelon, pers. comm.). Over the ringing period, both average daily minimum and maximum temperatures decreased significantly ($r^2 = 0.42$, df = 12, P = 0.0128, slope = -0.94 ± 0.32 (SE) and $r^2 = 0.65$, df = 12, P = 0.0005, slope = -1.33 ± 0.28 (SE), respectively; Fig. 2). Note that this is not a general pattern at a broader time scale, as no significant trend could be detected if years before and after the study period were included ($r^2 = 0.003$, df = 32, P = 0.7988 and $r^2 = 0.002$, df = 22, P = 0.8223 for average minimum and maximum temperatures, respectively; see Fig. 2). The three winters (1955/56, 1961/62 and 1963/64) when important cold spells occurred could not be considered, for two reasons: (i) hard frost not only induces displacement of the smallest individuals from northern to southern Europe, but is most likely to lead to major movements of virtually all individuals, whatever their size, that seek shelter in southern areas like the Camargue (Lebreton 1973, Ridgill & Fox 1990), and (ii) during these major cold spells the traps were at the main ice-free and food-rich sites of the area, which also most probably affected the trapability of some birds, that would otherwise never have entered the traps.

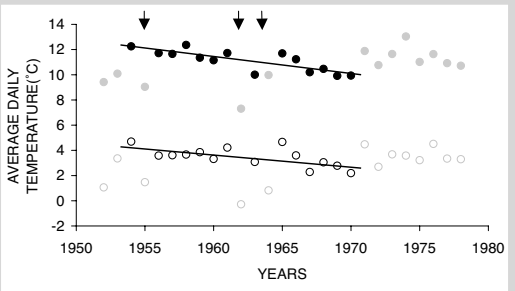


Figure 2. Average daily maximum (●) and minimum (○) temperature (in °C) in the Camargue during 1952-1978. Data concerning the main period of teal ringing at the Tour du Valat (1954-1971) are indicated in black, whereas data not used in the analyses, i.e. from before and after the main teal ringing period (or during the three major cold spells, indicated by arrows) are shown in grey. See text for statistics.

In addition to switching between winter quarters in mid-season forced by cold temperatures (which should be detected by studying the effect of December-February temperatures described above), teal may be affected by the temperatures they encounter during autumn migration in the North, and base their decision as to where to winter on these meteorological conditions. For this reason, we also tested the effect of annual average daily temperature in October-November (both minimum and maximum) in the Netherlands, namely at the Groningen meteorological Station (data provided by the Royal Netherlands Meteorological Institute) on teal body size, body mass and population structure in the Camargue. In all analyses, we first included the two variables in a General Linear Model, and deleted the potentially non-significant one through a stepwise backwards procedure (significance threshold $P < 0.05$). Camargue temperature data are referred to as 'winter temperatures', while Dutch data are referred to as 'autumn temperatures' below.

Raw data were used in the analyses, except when analysing variation of the sex and age structure of the population (i.e. proportion of males among first-year birds and among adults, and proportion of adults among males and females): in that case, proportions were arcsin-transformed before the analyses (Sokal & Rohlf 1995).

Results

The average wing length of teal a given season was never significantly related to average maximum daily autumn temperatures, but increased with increasing average maximum daily winter temperature, for all sex and age classes (Fig. 3). The pattern for average minimum daily temperature was the same (i.e. only a significant effect of Camargue winter temperatures, no signifi-

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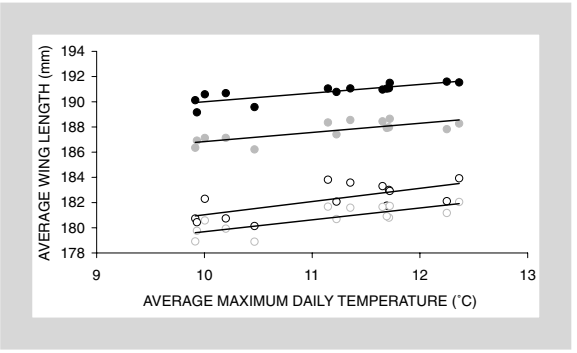


Figure 3. Relationships between average wing length (in mm) of male (●) and female (○) teal caught annually at the Tour du Valat and the average daily maximum temperature (in °C). Symbols for adults are in black, for first-year birds in grey. The relationships are significant in all cases (adult males: $r^2 = 0.68$, df = 12, P = 0.0003, slope = 0.07 ± 0.01 (SE); first-year males: $r^2 = 0.60$, df = 12, P = 0.0011, slope = 0.07 ± 0.02 (SE); adult females: $r^2 = 0.49$, df = 12, P = 0.0055, slope = 0.10 ± 0.03 (SE); first-year females: $r^2 = 0.62$, df = 12, P = 0.0008, slope = 0.09 ± 0.02 (SE)).

cant effect of Dutch autumn temperatures), although slightly less pronounced, except for adult females where it was not significant (adult males: $r^2 = 0.57$, df = 12, P = 0.0019, slope = 0.07 ± 0.02 (SE); first-year males: $r^2 = 0.39$, df = 12, P = 0.0162, slope = 0.07 ± 0.02 (SE); adult females: $r^2 = 0.26$, df = 12, P = 0.0621; first-year females: $r^2 = 0.39$, df = 12, P = 0.0174, slope = 0.08 ± 0.03 (SE)).

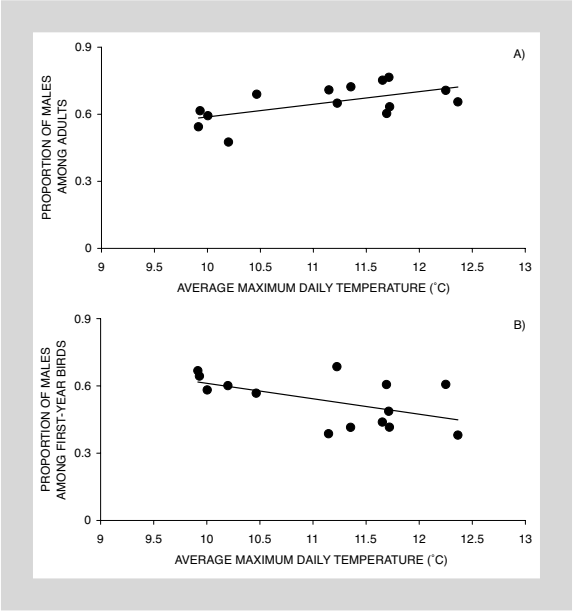


Figure 4. Relationships between the proportion of males among adults (A) or the proportion of males among first-year birds (B) and the average daily maximum temperature (in °C). The relationships are significant in both cases (see text).

No such relationship was found between average body mass of the birds and either average daily minimum or maximum, autumn or winter temperature (all $r^2 < 0.23$, df = 12, all P > 0.08).

The age structure of the population (i.e. proportion of adults either in males or in females) did not show any significant relationship with either average minimum or average maximum, autumn or winter temperatures (all $r^2 < 0.22$, df = 12, all P > 0.08). Conversely, there were more males among adults when average daily maximum winter temperature increased ($r^2 = 0.35$, df = 12, P = 0.025, slope = 0.34 ± 0.13 (SE)), with no significant effect of average daily maximum autumn temperature, and there tended to be fewer males among first-year birds when average daily maximum winter temperature increased ($r^2 = 0.29$, df = 12, P = 0.046, slope = -0.40 ± 0.18 (SE); Fig. 4), still with no significant effect of average daily maximum autumn temperature. There were no significant relationships between average minimum daily temperatures (neither during autumn nor during winter) and the proportion of males in either adults or juveniles (both $r^2 < 0.21$, df = 12, both P > 0.09).

Discussion

Recent analyses of bird ringing databases have highlighted major long-term changes in bird ecology and linked these changes to behavioural adaptations of the individuals to climatic change (e.g. McCarty 2001 for a review). Among these changes, range expansions and constrictions have been detected in many European species and hypothesised to result from changing climatic conditions and associated changes in the environment, either allowing or preventing individuals to use specific areas nowadays (e.g. Prop et al. 1998, Burton 1995, Sanz 2002).

In addition to changes in the overall range of a species, it may also be that some individuals, that were formerly limited to some parts of the species range because of their individual abilities and characters, now become able to use new areas because of environmental change. For example, global warming may allow (smaller) individuals most sensible to cold to start using the northernmost parts of the species range. The results of our study suggest that climate change may indeed affect the type of teal that is able to winter in a specific area.

The clearest relationship between the characters of teal ringed in the Camargue and temperature was for wing length: in all sex and age classes, wing length linearly increased with increasing average daily temperature, i.e. decreased over the 17-years with a decreasing trend in

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temperature. The relationship was only significant with mid-winter temperatures, not with temperatures recorded in late autumn further north on the flyway: this suggests that depending on the weather and on their size (i.e. ability to cope with cold temperatures) teal may decide to switch from one winter quarter to another in the middle of the season, and provides no support to the idea that these birds select their winter quarter on the basis of the meteorological conditions they encounter during autumn migration.

Despite the fact that the same professional ringers examined all the birds, the relative contribution of each of them changed over the course of the study, and this may gradually have led to an observer-induced change in wing length. Examination of the ringing sheets reveals that a total of 36 people ringed at least one teal. However, just seven ringers measured 89.14% of the birds for which wing length and ringer name was known. For each sex and age class, and for each year, the average wing length and number of birds measured by these experienced ringers are given in Appendix I. It is clear that different teams of observers followed each other over the 17 years of activity, and that differences between observers existed in some years. However, it was not possible to detect a clear observer effect that may have caused a gradual change in the wing length measured; differences between observers may be significant during some years but not in others (e.g. differences between measurements made by Ho and Mü at the beginning of the period, in all sex and age classes), or even be in opposite directions (e.g. larger average value for adult females measured by Ko than by Jgw in 1967 and 1968, but the reverse in 1970). In addition, differences between observers never explained a large proportion of the variance in wing length. Furthermore, for Ko, the observer that was active over the largest number of years, a significant decrease in measured wing length was observed over years in all age and sex classes except adult males, where the pattern was the same but not significant (Spearman rank correlations: adult females: $r_s = -0.96$, $N = 7$, $P < 0.05$; adult males: $r_s = -0.43$, $N = 7$, $P > 0.33$; juvenile females: $r_s = -0.90$, $N = 7$, $P < 0.05$; juvenile males: $r_s = -0.75$, $N = 8$, $P < 0.05$; for each age and sex class, only years when more than 30 individuals were measured by this observer were included in the analysis). It is therefore most unlikely that the observed pattern simply was caused by an observer effect.

It is also true that teal wing length varies across months in winter (Fox et al. 1992; M. Guillemain, A. Johnson & G. Simon, unpubl. data). However, most teal in the Camargue were caught in December-January (i.e. 62.6% ± 5.9% (SE), N = 14 years), and in no sex or age class did the proportion of birds caught in December-January show a significant trend over years (all $r^2 < 0.12$, df = 12, all $P > 0.22$). It is therefore very unlikely that the observed pattern of wing length variation over time was the consequence of a change in the distribution of teal catches over the winter.

Winter temperature data used in our study refer to the December-February period, i.e. the core of winter, when teal are most numerous. During this period, moulting has been completed by virtually all teal (M. Guillemain, pers. obs. based on the Tour du Valat database), so the observed pattern is very unlikely to be the consequence of negative effects of cold weather on feather growth.

Rather, we hypothesise that the relationship between teal wing length and temperature was genuine, i.e. that climate affected the type (i.e. size) of teal wintering in the Camargue: the colder the temperature, the smaller the birds, which also accords with the generally larger size of eastern, and potentially northern, teal (Cramp & Simmons 1977). Given the fact that male teal are larger than females, the result that more females were captured within adults during colder winters is consistent with the above pattern. The reason why this was not the case in juveniles is unclear, since juvenile males also are larger than juvenile females. It may be that other factors, such as dominance relationships for example, interplay with the effect of climate: in wigeon *Anas penelope* Campredon (1983) described a differential distribution of wintering individuals throughout Europe, with more adult males in the north-east and more females and juveniles in the south-west. If the pattern is the same in teal, then it may seem natural that climatic changes have the largest effect on the sex ratio in adults because the ranges of juvenile males and juvenile females are more similar to each other than the ranges of adult males and adult females, and most of the juveniles already winter in the south-west. The effect of changing climate on teal population structure would require further investigation, using data from distinct wintering quarters along a north-south gradient.

In a given winter quarter, one would expect that the average size of individuals should increase with decreasing temperature, since it is easier for larger birds to cope with colder climate. The pattern we observed in the Camargue was the opposite. However, we hypothesise that the negative trend in the Camargue temperature over years reflected a more general trend in the climate of teal winter quarters further north that forced the smallest individuals to move south to the Camargue, which played the role of a refuge (as already observed during cold spells, e.g. Tamisier & Dehorter 1999). Support to this

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hypothesis is given by the positive relationship between average maximum daily temperature in the Camargue and in Strasbourg, northeast France ($r^2 = 0.52$, df = 12, P = 0.004, slope = 1.21 ± 0.32; data from the NOAA - NCDC - Global Climate Observing System (GCOS) - GCOS Surface Network (GSN); avaliable at http://www.ncdc.noaa.gov/servlets/gsn). Therefore, the smallest teal that could not afford to spend the winter further north when the average temperature decreased would come to the Camargue to find shelter.

Given that the climate is warming globally, reversing the pattern recorded in this study would suggest that the smallest teal would gradually be able to remain further north during the winter. This would not necessarily affect negatively the overall size of teal populations in Europe, but their distribution over countries may change. Such large-scale displacements of duck wintering quarters in Europe have already been documented (Svazas et al. 2001). They may become more pronounced in the future, inducing new challenges to wildlife biologists. A new research program on teal ecology and movements was launched in 2002, which we hope may provide a better understanding of the factors affecting teal distribution throughout Europe.

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Appendix 1

Wing measurements and test of the observer effect (annual mean ± SE), with number of birds given in brackets and observers indicated by initials at the top of columns. Only observers that measured more than 5% of the total number of individuals are considered for each sex and age class, hence data are missing in some columns in some cases. For a given year and observer, data are included in the inter-observer comparison only if more than 30 birds were measured, hence comparisons are missing for some years.

	Observers							GLM results	
Year	Ha	Ho	Jgw	Ko	Ku	Mü	Ps	P-value	% variance explained
				Adult females					
1954		184.7 ± 2.3 (3)				181.8 ± 0.5 (55)			
1956		183.2 ± 0.5 (73)				183.0 ± 0.6 (46)		NS	
1957		182.4 ± 0.4 (129)				183.8 ± 0.3 (222)		0.002	2.60%
1958		183.6 ± 0.4 (91)			184.2 ± 0.3 (235)			NS	
1959		183.6 ± 0.7 (35)			183.6 ± 0.2 (268)			NS	
1960		183.2 ± 1.4 (8)			183.8 ± 0.5 (59)		183.2 ± 0.6 (52)	NS	
1961		182.5 ± 1.3 (10)		182.6 ± 0.5 (74)	188.0 (1)		183.4 ± 0.4 (132)	NS	
1963	183.0 ± 2.9 (2)			182.5 ± 0.3 (220)			181.8 ± 1.1 (13)		
1965	183.4 ± 1.5 (7)			181.8 ± 0.4 (98)					
1966	181.7 ± 0.6 (52)			182.4 ± 0.3 (166)				NS	
1967	180.2 ± 0.3 (194)		180.1 ± 0.5 (77)	181.2 ± 0.2 (327)				0.005	1.80%
1968	178.3 ± 0.7 (33)		180.5 ± 0.7 (33)	180.8 ± 0.6 (39)				0.015	7.90%
1969			180.8 ± 0.3 (158)	183.5 ± 1.4 (8)					
1970			181.4 ± 0.2 (276)	180.4 ± 0.3 (155)				0.011	1.50%
				Adult males					
1954		191.9 ± 1.5 (7)				191.4 ± 0.4 (130)			
1956		190.9 ± 0.3 (203)				190.9 ± 0.3 (183)		NS	
1957		190.2 ± 0.2 (294)				190.9 ± 0.1 (758)		0.018	0.50%
1958		191.9 ± 0.3 (151)			191.3 ± 0.2 (418)			NS	
1959		190.0 ± 0.6 (49)			190.9 ± 0.2 (663)			NS	
1960		191.4 ± 1.3 (10)			191.9 ± 0.5 (59)		191.5 ± 0.3 (243)	0.025	1.70%
1961		191.8 ± 0.9 (19)		191.1 ± 0.3 (171)			191.8 ± 0.3 (195)	NS	
1963				190.9 ± 0.2 (328)			189.0 ± 2.3 (3)		
1965				190.7 ± 0.3 (177)					
1966				191.3 ± 0.2 (348)					
1967			189.9 ± 0.4 (117)	191.6 ± 0.3 (235)				< 0.001	3.70%
1968			188.7 ± 0.4 (84)	190.6 ± 0.5 (54)				0.006	5.50%
1969			190.0 ± 0.3 (138)	190.9 ± 0.8 (26)					
1970			188.7 ± 0.2 (554)	190.4 ± 0.3 (166)				< 0.001	3.10%

Year	Observers							GLM results	
	Ha	Ho	Jgw	Ko	Ku	Mü	Ps	P-value	% variance explained
Juvenile females									
1954		182.7 ± 1.4 (8)				181.0 ± 0.5 (74)			
1956		180.7 ± 0.2 (427)				181.0 ± 0.2 (476)		NS	
1957		181.3 ± 0.1 (1130)				181.7 ± 0.1 (3449)		0.012	0.10%
1958		181.7 ± 0.2 (494)			182.3 ± 0.1 (1390)	185.0 (1)		0.003	0.50%
1959		180.6 ± 0.3 (159)			182.0 ± 0.1 (1537)			< 0.001	1.10%
1960		182.1 ± 0.7 (37)			181.6 ± 0.2 (546)		181.7 ± 0.3 (211)	NS	
1961		181.6 ± 0.5 (67)		182.0 ± 0.4 (114)			181.7 ± 0.2 (696)	NS	
1963				181.0 ± 0.2 (376)			181.2 ± 0.7 (36)	NS	
1965				181.4 ± 0.4 (99)					
1966				181.0 ± 0.4 (112)					
1967				180.7 ± 0.2 (364)					
1968				178.7 ± 0.5 (55)					
1969				180.5 ± 1.0 (17)					
1970				180.1 ± 0.3 (183)					
Juvenile males									
1954		189.2 ± 1.1 (13)				188.0 ± 0.4 (114)			
1956		187.1 ± 0.2 (349)				188.6 ± 0.2 (495)		< 0.001	3.30%
1957		188.2 ± 0.1 (792)				188.5 ± 0.1 (2656)		NS	
1958		188.4 ± 0.2 (307)			188.3 ± 0.2 (839)	192.0 (1)		NS	
1959		188.2 ± 0.6 (42)			188.8 ± 0.1 (966)			NS	
1960		189.2 ± 0.9 (20)			188.4 ± 0.2 (385)				
1961		188.6 ± 0.6 (51)		188.0 ± 0.4 (79)				NS	
1963				187.6 ± 0.2 (535)					
1965				188.1 ± 0.3 (172)					
1966				188.0 ± 0.2 (268)					
1967			187.0 ± 0.3 (149)	187.8 ± 0.2 (691)				0.014	0.70%
1968			186.2 ± 0.4 (91)	187.2 ± 0.3 (131)				NS	
1969			186.2 ± 0.2 (330)	187.0 ± 0.7 (37)				NS	
1970			186.9 ± 0.2 (149)	187.1 ± 0.2 (314)				NS	

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