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CIRCANNUAL CHANGES IN THE SEXUAL SIZE DIMORPHISM IN STREPTOPELIA DECAOCTO (AVES: COLUMBIDAE)

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Abstract. Circannual changes in the body weight and sexual size dimorphism in the Collared Dove *Streptopelia decaocto* were studied. Circannual changes in the body weight in both males and females were found to be marked, different from each other and apparently adaptive. On the other hand, circannual changes in the sexual size dimorphism were also found to be marked, but non-adaptive. Factors affecting the phenomena under study are discussed.

INTRODUCTION

Animal species have been traditionally considered either sexually dimorphic or sexually monomorphic in size. It was Selander (1966, 1971, 1972) who showed that this a-priori assumption may not be true, and that the degree of the sexual size dimorphism can considerably vary with respect to different organs within a species. Selander's suggestion has been later corroborated in several studies (e. g. Andersson and Wester 1971, Kushlan 1977, Weatherhead 1980, Johnston and Fleischer 1981, Mlíkovský and Piechocki 1983, in press, Piechocki 1984). In addition, Mlíkovský and Piechocki (1983b), studying the European Common Bussard (*Buteo buteo*) could show that the degree of the sexual size dimorphism can considerably vary circannually.

Their observations will now be tested on the European Collared Dove *Streptopelia decaocto* (Frivaldszky, 1838). Simultaneously, as only scarce data regarding circannual changes in body weight in the Columbidae (Grundová 1965, Ljunggren 1968, Dvořáková-Grundová 1970, Rana 1975), as well as regarding body weights of the Collared Doves themselves (Kroneisl-Rucner 1957, Niethammer 1962, Dekker 1963, Grundová 1965, Lachner 1965, Dvořáková-Grundová 1970, Creutz and Piechocki 1970; cf. also Hofstetter and Scherner 1980) have so far been published, the present paper will contribute also to these more specific problems.

MATERIALS AND METHODS

All the Collared Doves studied in this paper (180 males and 165 females) were collected in the Prague Zoological Garden (ZOO Praha) during the year 1976 by Petr Švec and Jan Dřevo. In this area Collared Doves are abundant throughout the year, are non-migratory, and because they mostly feed on corn supplied to various ZOO animals, they always have food ad libitum (Švec 1978).

All birds were killed before weighting and weighted in fresh state by Petr Švec on the "Labora" weight with the accuracy to 0.1 gramm. Crop contents were removed before weighting. Sex was estimated by dissection ofter weighting. Age of the collected birds was estimated ecording to characters given in Lachner (1965) and only adult birds, i. e. birds older than 1 year (age classes II and III of Lachner 1965) were included into the further analysis.

The data obtained were further elaborated by Jiří Mlíkovský. For every month, mean body weight (x), its standard error (s_x), standard deviation (s_{n-1}), its standard error (S_s), and coefficient of variation (CV) were calculated for each sex separately using standard formulas of mathematical statistics (see, e. g., Sokal and Rohlf 1969, Weber 1980). Curves in the Figures 3,4, and 5 were calculated using the method of gliding means (Gebelein 1951). The dimorphism index (D.I.) was calculated as D.I. = m/f, where m = mean body weight of males, and f = mean body weight of females, respectively, and tested with the t-test (Sokal and Rohlf 1969).

RESULTS AND DISCUSSION

Circannual changes of the body weight in the Collared Dove are presented in Figures 1 and 2, respectively (see Tables 1 and 2 for exact data). Interestingly enough, their general tendencies in males and females are quite different (cf. Fig. 3), so that the sexual size dimorphism strongly varies during the year in Collared Dove (see Fig. 4 and Tab. 3).

Using these findings, we shall now attempt to discuss both the basic hypotheses concerning the essence and importance of the sexual size dimorphism which are a-priori applicable to doves, namely the ecological and the sexual one.

According to the ecological hypothesis, different sizes of sexes within a species evolved for enabling their niche separation (e. g. Rand 1952, Selander 1966, 1972, Andersson and Norberg 1981). Indeed, this suggestion has been later documented on various vertebrates, especially birds (e. g. Hö-

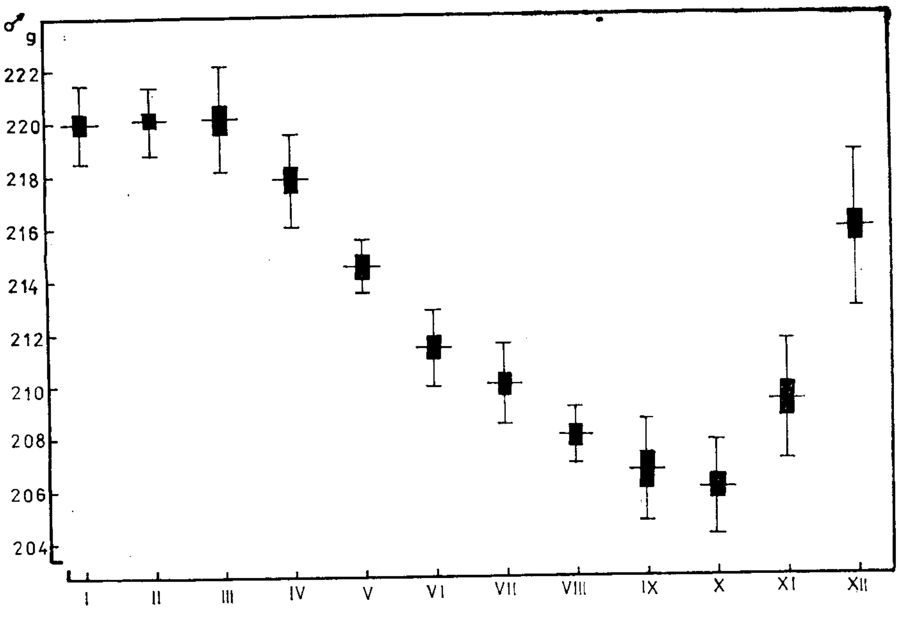

Fig. 1. Circannual changes in body weight of male Collared Doves. Given are mean, its standard error, and standard deviation, Based on data from the Table 1.

glund 1964, Storer 1966, Eahart and Johnson 1970, Brosset 1973, Snyder and Wiley 1976, Mueller et al. 1981).

No such effect is probable in the Collared Dove, although Helešic (1981) detected slight differences between the sexes of this species. He noted, however, that these differences are apparently caused by their different feeding site

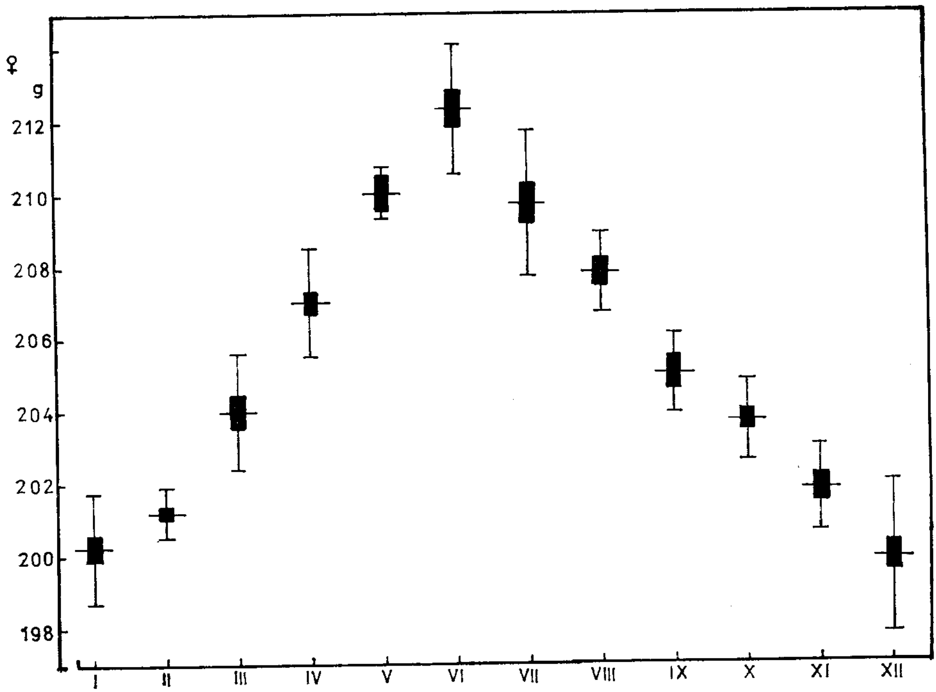

Fig. 2. Circannual changes in body weight of female Collared Doves. Based on data from the Table 2. See Fig. 1 for explanation.

selection. Morover, he found no correlation between food composition and body size in his study population of the Collared Dove. Although other authors dealing with the study of the food composition of the Collared Dove did not consider sex differences (e. g. Kovacević and Danon 1951, 1957, Fric 1954, Feriancová 1955, Barthos 1957, Tutman 1960, Szlivka 1965, Soviš and Vallo 1966, Bičík and Směšná 1971, 1972, Rekasi 1975, Nowak 1975), we consider Helešic's (1981) results convincing enough to exclude the ecological hypothesis of the sexual size dimorphism in the Collared Dove.

On the other hand, our data seem to agree more closely with the hypothesis which tries to explain sexual size dimorphism in the terms of sexual selection (e. g. Darwin 1871, Nekrasov 1927, Huxley 1938, Kistjakovskij 1958, Amadon 1959. Davitašvili 1961, Mayr 1972, Trivers 1972, Searcy 1982, and many others). However, as we shall explain further below, we believe that the sexual size dimorphism is not selected for in the Collared

Table 1. Body weight statistics in male Collared Doves.
Weights in gramm. CV in %

month	$\bar{x}$	$s_{\bar{x}}$	s_{n-1}	s_s+	CV	s_{CV}	n
I	219.91	0.327	1.427	0.231	0.649	0.105	19
II	221.14	0.270	1.210	0.191	0.547	0.086	20
III	221.39	0.528	1.974	0.373	0.892	0.169	14
IV	217.83	0.507	1.829	0.359	0.840	0.165	13
V	214.52	0.439	0.983	—	0.458	0.145	5
VI	211.42	0.399	1.437	0.282	0.680	0.133	13
VII	209.71	0.395	1.528	0.279	0.729	0.133	15
VIII	208.45	0.379	1.073	—	0.515	0.129	8
IX	206.66	0.676	1.912	—	0.925	0.231	8
X	206.26	0.419	1.778	0.296	0.862	0.144	18
XI	209.23	0.594	2.300	0.420	1.099	0.201	15
XII	215.83	0.516	2.918	0.365	1.352	0.169	32
I—XII	214.32	0.425	5.708	0.301	2.663	0.140	180

+) Not calculated for too small samples.

Dove, i. e. that it is non-adaptive (but not maladaptive!) (cf. Gould and Lewontin 1979, and Hilborn and Stearns 1982 for recent critics of the adaptationists program). On the contrary, we are convinced in the adaptiveness of circannual body size changes wihin both sexes of the Collared Dove separately.

Let us take males at first. Their body weight falls to its minimum in October, then rises fastly up to its maximum which it reaches in January through March. Since April their body weight falls again slowly to its minimum in October (see Fig. 1). Now, we have to search for the reasons for the location of these

Table 2. Body weight statistics in female Collared Doves.
Weights in gramm. CV in %

month	$\bar{x}$	s_x	s_{n-1}	s+	CV	s_{CV}	n
I	200.25	0.330	1.512	0.233	0.755	0.117	21
II	201.18	0.172	0.686	0.121	0.341	0.060	16
III	203.98	0.445	1.603	0.314	0.786	0.154	13
IV	207.00	0.444	1.471	0.314	0.711	0.152	11
V	210.02	0.288	0.705	—	0.336	0.097	6
VI	212.29	0.508	1.760	0.359	0.829	0.169	12
VII	209.69	0.547	1.973	0.387	0.941	0.184	13
VIII	207.80	0.410	1.085	—	0.521	0.140	7
IX	205.02	0.459	1.123	—	0.548	0.158	6
X	203.69	0.244	1.120	0.173	0.550	0.085	21
XI	201.83	0.362	1.201	0.256	0.595	0.127	11
XII	199.88	0.396	2.094	0.280	1.047	0.140	28
I—XII	204.03	0.340	4.364	0.240	2.139	0.118	165

+) Not calculated for too small samples.

cardinal points. There are, we believe, three a-priori reasonable explanations for high body weights of the male Collared Doves in winter months, as follows:

(1) Large body size provides advantage during severe winter weather. — Although the mortality of Collared Doves seems be largest in winter (cf. R o s t

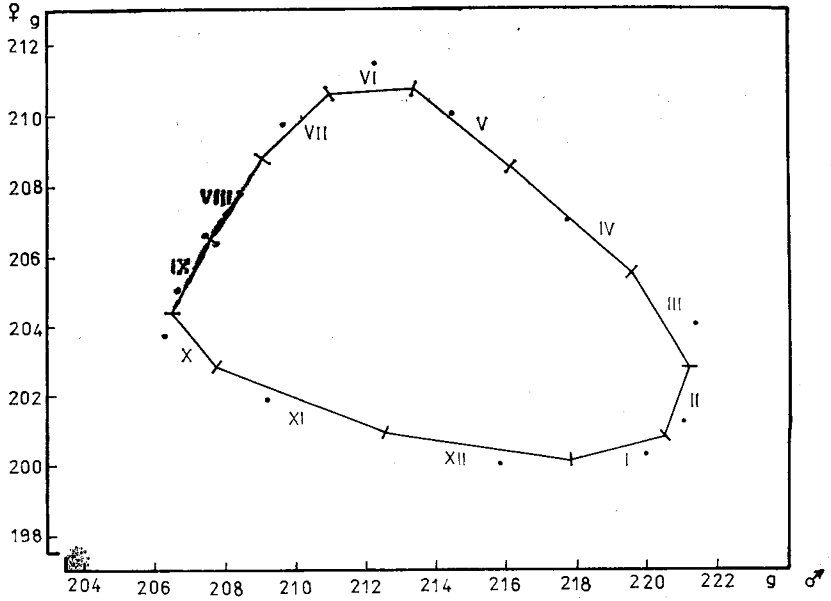

Fig. 3. Circannual changes in the relation between absolute body weights of male and female Collared Doves. Based on the data from the Tables 1 and 2.

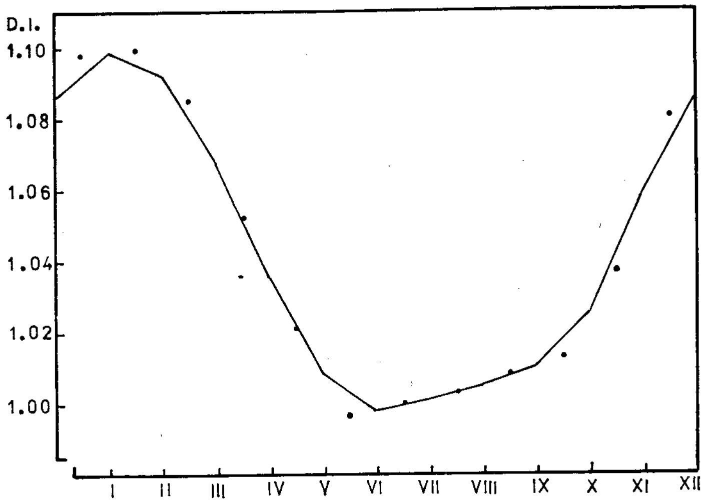

Fig. 4. Circannual changes in the sexual size dimorphism in the Collared Dove. Based on data from the Table 3.

Table 3. Circannual changes in the sexual size dimorphism in Collared Dove. Calculated from data given in Tables 1 and 2.
Significance: ++ = $p < 0.01$, + = $p < 0,1$, — = $p > 0.1$

month	D. I.	Sign.
I	1.098	++
II	1.099	++
III	1.085	++
IV	1.052	++
V	1.021	++
VI	0.996	—
VII	1.000	—
VIII	1.003	—
IX	1.008	—
X	1.013	++
XI	1.037	++
XII	1.080	++
I—XII	1.050	++

1957, Dyrcz 1961, Nowak 1965, 1976, Gnielka 1975), larger individuals are in general less vulnerable to cold (cf. Pomarnacki 1960), and larger individuals of the Collared Dove had usually more food in crop than smaller ones (Helešic 1981). This may enable them to survive long cold winter nights better, because they begin to root at evening with full crops and digest their content till next morning (Murton et al. 1964, Bičík and Směšná 1971, Helešic 1981). Despite of this we consider this explanation improbable, because female Collared Doves reach during winter months their body weight minimum, and all of the above mentioned selection factors should work similarly on both males and females, the more that they build large common flocks during winter (cf., e. g., Feriancová 1955, Lachner 1963, Nowak 1965, Bičík and Směšná 1971, Hudson 1972, Reichholf 1976, Švec 1978, Helešic 1981).

(2) Large body size is advantageous in intrasexual selection. — The Collared Dove is monogamous, territorial species in which males are responsible for the gain and maintenance of the breeding territory (cf., e. g., Bodenstein 1949, Hofstetter 1954, Tomasz 1955, Nowak 1965). Hence, larger males probably have more success in gaining a territory (or a better territory) than smaller ones. Because the area for breeding is apparently limited in ZOO Praha, and because there is, consequently, a relatively large floating population of Collared Doves there (see Švec 1978), it is probable that a (how strong?) intrasexual selection between males occurs, in which larger males may be more advantageous. Because the time of mating coincides well with the maximum body size in studied Collared Dove males, we believe that the hypothesis under discussion may be one of explanations for their high body weights during January through March. This is indirectly supported also by Grundová (1965, Dvořáková-Grundová 1970) who found a correlation between the body size increase and the increase in gonadal activity in male Collared Doves. This is not surprising because both the increase of gonadal

activity (M u r t o n and W e s t w o o d 1977) and body weight changes (P a l y a et al. 1983) are controlled by light cycle in columbids.

(3) Larger males are preferred by females during the intersexual selection. – It has been proved experimentally that columbid females select their mates according to their individual, personal characteristics (M o r r i s and E r i c k s o n

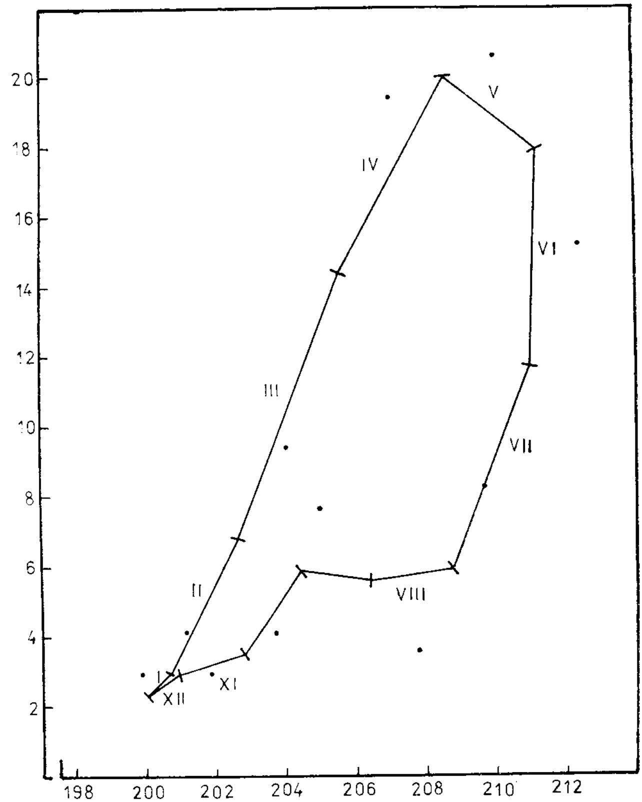

Fig. 5. Circannual changes in the relation between the frequency of breeding and absolute weights of female Collared Doves. Based on data from the Tables 3 and 4.

1971, B u r l e y 1977, 1981, B u r l e y and M o r a n 1979). Although we dispose of no empirical data regarding whether body size belongs to the characters selected for by Collared Dove females or not, it is probable that intersexual selection accounts for the large body size in male Collared Doves during winter months, too.

Let us now turn to the question why a decrease of body weight occurs during spring and summer months in male Collared Doves. Because food is always available ad libitum for Collared Doves in ZOO Praha (Š v e c 1978), food shortage cannot account for these low weights. Another possible explanation could be molt, because it is energetically rather expensive for most birds (cf. P a y n e 1972, D o l' n i k 1975, M u r t o n and W e s t w o o d 1977), but

Table 4. Breeding season of the Collared Dove in ZOO Praha. From Švec (1978)

month	n	%
I	3	2.50
II	5	4.17
III	15	12.50
IV	28	23.33
V	25	20.83
VI	15	12.50
VII	8	6.67
VIII	3	2.50
IX	8	6.67
X	5	4.17
XI	2	1.67
XII	3	2.50
I—XII	120	100.01

Columbidae are exceptional in this respect. As documented by Murton and Westwood (1977), production of milk by which columbids feed their young reduced their need for energy peaks (see also Brisbin 1969), and enabled them, consequently, to breed and molt partly simultaneously (see, e. g., Murton and Westwood 1977, and Švec 1978). Hence, the energy requirements for molt seem not to cause the decline of body weight observed during summer and fall in male Collared Doves. Due to the absence of other reasonable hypotheses, we are, then, forced to leave this problem open.

Let us now to discuss reasons for the seasonal changes in body weight in female Collared Doves. Their body weight cycle reachs its peak in June, i. e. in the time when the weight of males already heavily declines. For this reason we see no way how this peak could be correlated with any climatic factor. Because the time when female Collared Doves reach their body weight maximum coincides with their preferred breeding season (cf. data in Švec 1978 and our Fig. 5), it seems highly probable that the reasons for this mode of seasonal body size changes are to be searched for in the reproduction (sensu lato). Briefly summarized, larger females have in comparison with smaller ones the following respective advantages:

(1) They are able to breed earlier in the year. — This has been well documented for various bird species (e. g. Murton and Isaacson 1962, Murton et al. 1963 a, b, Ryder 1970; cf. also Gates and Woehler 1968, Milne 1976 and Woodall 1981). This can be indirectly supported by our data (Fig. 5), too, which show a clear linear positive correlation between the increasing frequency of breeding and the increasing mean body weight of female Collared Doves in ZOO Praha. Early breeding is advantageous because early fledged young have better chance for subsequent survival, as has been evidenced in *Columba* spp. (Murton 1961, 1966), as well as in several non-columbid bird species (Perrins 1963, 1966, Kluijver 1971, and others).

(2) They lay larger eggs. — This has been evidenced, e. g., by Väisäinen 1969, Väisäinen et al. 1972, Murton et al. 1974, Lundberg and Väi-

säinen 1979 and Mills 1979. The advantage of this consists in the positive correlation between the survival of young and the size of eggs from which they hatched (cf., e. g., Parsons 1970, 1972, 1975, Nisbet 1973, 1978, Schifferli 1973, Davis 1975, Lundberg and Väisäinen 1979, Schreiber et al. 1979, Boersma et al. 1980, Ankney 1980, Coulter 1980, Mänd 1980, 1983, Moss et al. 1981, Moss and Watson 1982).

We believe that these selective advantages are convincing enough to explain why female Collared Doves reach their maximum body weight during the peak of their breeding season. However, similarly as in males, we are not able to find any reasonable explanation for the marked weight decrease after the breeding season, especially in winter (cf. the discussion of this problem in the section on males), and leave, hence, the latter problem open in females, too.

CONCLUSIONS

Seasonal changes in the body weight and sexual size dimorphism were studied in the Collared Dove *(Streptopelia decaocto)* population inhabiting Prague Zoological Garden. It is concluded that:

(1) Changes in the sexual size dimorphism are marked, but not adaptive.

(2) Changes of the body weight of each sex separately are adaptive, though possible explanations were found for maximum weights only, not for minimum ones.

(3) Maximum body weight of males coincides with the time they compete for territories (intrasexual selection), and large size belongs, perhaps, to characters preferred by females during their mate selection (intersexual selection).

(4) Maximum body weight of females coincides with their main breeding season. This is probably because (a) larger females breed earlier and earlier fledged young have better probability to survive, and (b) larger females lay larger eggs and young hatched from larger eggs survive better.

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