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GENERAL BIOLOGY

Stress and Social Behavior in a Natural Population of Tamarisk Jirds

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Until recently, the relationship between the stress level and individual characteristics of social behavior was mainly studied in the laboratory. Field studies were few (for example, [14]), which is mainly explained by limited possibilities of estimating the stress level by the levels of hormones in the blood plasma. The development of methods of the assessment of steroid hormones in feces, as well as the validation of adequacy of noninvasive approaches to the assessment of the endocrine status [1, 9, 13], considerably extended the possibilities of studying the stress level in mammals in their natural environment. Even the earliest results obtained using these methods revealed a diverse pattern of relationships between the hormonal and social statuses in various species [5, 6, 8].

In this work, we, using noninvasive methods of assessment of corticosterone and testosterone amounts in feces, pioneered in the analysis of the relationship between the functional activity of the adrenal cortex and gonads and the social status of male tamarisk jirds (*Meriones tamariscinus*) studied in their natural environment.

The material was collected from May 3 to June 22, 1998 (during the reproductive period) in southern Kalmykia. Jirds were captured and individually marked in stationary areas. Based on the data of repeated captures of marked jirds, we estimated the sizes of their action areas (by the number of used traps) and their overlap (by the percentage of traps visited by a given jird and other jirds out of the total number of traps only visited by the given jird). The social status was determined by 15-min experimental dyadic encounters of males unfamiliar to one another, whose action areas did not overlap and were not neighboring. The experimental encounters were conducted in the field, 1–2 h after capture. For each male, we estimated the following parameters: frequency of threats, aggression, defensive behavior, and frequency of avoidance. Males were divided into aggressive (which initiated aggression) and nonaggressive (which did not initiate aggression) ones. If the difference between offensive and passively defensive behavior was positive in a male, this male was considered dominant; if negative, subordinate.

To assess the endocrine status, feces were immediately collected from the traps in which captured jirds were kept for no more than 3 h. Feces were dried to a constant weight at 30–40°C. Dry weighted samples of feces were homogenized in distilled water and centrifuged. Steroids were extracted from the supernatant by diethyl ether. Extracts were evaporated, and the dry residue was diluted with a phosphate buffer. The concentrations of corticosterone and testosterone were determined by a radioimmune method as recommended by the manufacturers of antibodies Anti-Cort and Anti-T (Sigma).

The contents of corticosterone and testosterone in feces of males considerably varied (from 54 to 420 ng/g (N = 66) and from 39 to 912 ng/g (N = 64), respectively). Differences between individuals in both corticosterone and testosterone concentrations were reproducible in repeated samples ($F_{6.27}$ = 2.72; p = 0.0337 and $F_{6.27}$ = 3.25; p = 0.0154, respectively); i.e., the hormonal status of males appeared to be a stable individual trait. The concentrations of corticosterone and testosterone did not correlate (R^2 = 0.02; $F_{1.59}$ = 1.27; p = 0.2642).

The content of corticosterone in feces inversely depended on the size of the action area (Fig. 1a, R_s = –0.60, p = 0.0227) and the degree of overlap of the action area (Fig. 1b, R_s = –0.84, p = 0.0190), i.e., indices reflecting the mobility and freedom of moving for males. The content of testosterone in feces did not correlate with specific individual characteristics of space use (Figs. 1a, 1b).

The level of corticosterone in dominant males was lower than in subordinate males (185 ± 27 ng/g, N = 11 and 282 ± 33 ng/g, N = 7, respectively; Mann–Whitney test: U = 17.0, p = 0.0515) and negatively correlated

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with the frequency of initiated threats (Fig. 1c, $R^2 = 0.22$, $F_{1.16} = 4.51$, $p = 0.0497$). We found that the frequency of defensive acts ($R_s = 0.29$, $p = 0.2364$) and the level of aggression ($R_s = 0.02$, $p = 0.9283$) were not related to the level of corticosterone. We also found no differences between aggressive and nonaggressive males (224 ± 28 ng/g, $N = 6$, and 222 ± 33 ng/g, $N = 12$, respectively; Mann–Whitney test: $U = 34.5$, $p = 0.8882$).

The content of androgens in feces did not correlate with any quantitative behavioral index of males; the dominant and subordinate, as well as aggressive and nonaggressive, males did not differ from each other in this respect.

Our data indicate a high diversity of the studied natural group of male jirds with respect to the secretory activity of the adrenal cortex and gonads. The individual endocrine status was steadily maintained during the middle of the reproductive period. Earlier, stable individual differences in the concentration of corticosterone in feces were detected in a natural population of red voles [5].

The content of corticosterone in feces of male jirds negatively correlated with a set of indices reflecting their social competitiveness, namely, with the area and freedom of moving and social dominance under the conditions of experimental conflict. The level of corticosterone was not related to aggressiveness. These data agree with both the data obtained on free-ranging red voles, in which the level of corticosterone in feces was lower in males moving over long distances [5], and the data on the inverse relationship between the social status (but not aggressiveness) and the blood-plasma level of glucocorticoids in free-ranging male jaguar baboons [14].

Conversely, in African hunting dogs [8] and ring-tailed lemurs [6], hydrocortisone level was higher in dominants and the most aggressive individuals. These opposite trends may reflect radically different ways of the formation of social-dominance relations: the maintenance of a high status at the expense of aggressiveness is associated with heavy physical and emotional loads, i.e., stress [6, 8].

In the wild, tamarisk jirds are characterized by a solitary and reclusive way of life; they do not form stable teams; and contacts between jirds are rare, transient, and typically not intense [4]. In tamarisk jirds, the individual differences in functional activity of the HPAA are rather the cause than the effect of different social competitiveness. This type of causal relationship between the stress level and social status was demonstrated in experiments on laboratory rodents: a stable activation of the HPAA reduces the chance to win in a social conflict, even if the experimental animals have been kept separately [3, 10].

Regardless of the widespread ideas on the effect of androgens on male aggressiveness [12, 15], the content of testosterone in feces is not correlated with the behavioral indices studied in tamarisk jirds. These results agree with some recent data, in particular, the data obtained using noninvasive technologies. These data show that the basal level of testosterone in feces does not allow one to predict whether an individual wins or loses in a social conflict [7]. This may be caused by the presence of critical ontogenetic stages [15], beyond which sex hormones either have no effect on behavior or they affect behavior at significantly higher concentrations (beyond the natural range of variation of the testosterone content in blood) [2, 11].

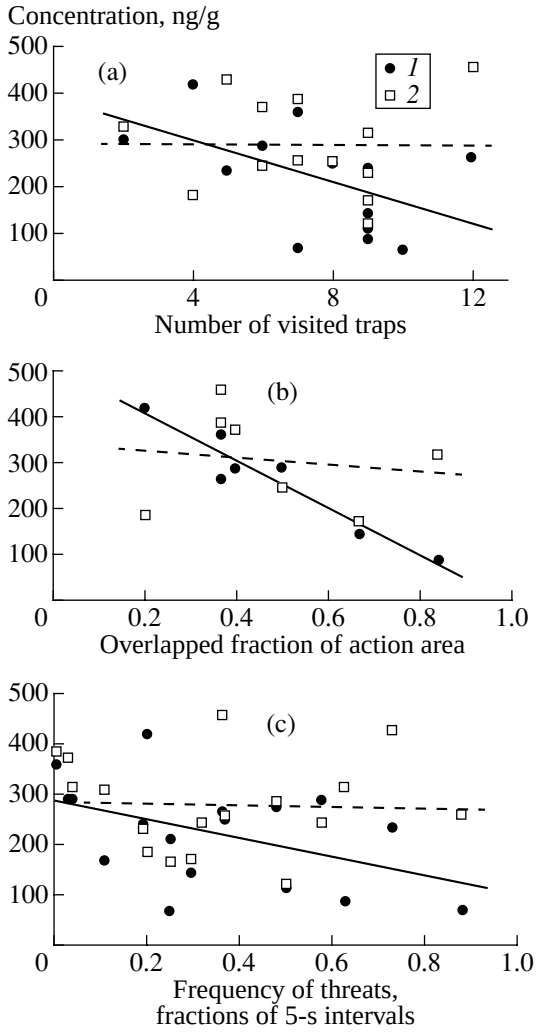

Fig. 1. Relationship between concentration of hormones and (a) action area, (b) overlap of action areas, and (c) frequency of threats; *1*, corticosterone; *2*, testosterone.

The lack of association between the concentrations of corticosterone and testosterone indicates that the detected relationship between the stress level and social status (but not aggressiveness) of jirds is not a side effect of reciprocal relationships between the adrenocortical activity and secretion of androgens. The persistent diversity of males with respect to the functional activity of the HPAA that can be formed in response to

a wide range of stress factors creates the prerequisites for regulating interindividual relations. In the population of the tamarisk jird, a species with a solitary mode of life, this is expressed as follows: jirds with the lowest stress level possess the highest social competitiveness.

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