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Is a wild mammal kept and reared in captivity still a wild animal?

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Abstract

This study compared domestic guinea pigs (*Cavia aperea* f. *porcellus*; DGP) and two different populations of the wild cavy (*Cavia aperea*), its ancestor, to examine whether rearing of wild mammals in captivity affects their behavior and physiological stress responses. One population of wild cavies consisted of wild-trapped animals and their first laboratory-reared offspring (WGP-1). The animals of the other population were reared in captivity for about 30 generations (WGP-30). The spontaneous behavior of each of six groups of WGP-1 and WGP-30 and nine groups of DGP, each consisting of one adult male and two adult females, was analyzed quantitatively. Blood samples of the males were taken to determine cortisol, epinephrine, and norepinephrine concentrations. In addition, the exploratory behavior of 60-day-old male WGP-1, WGP-30, and DGP was investigated in an exploration apparatus. The domesticated animals displayed significantly less aggression, but significantly more sociopositive and male courtship behavior than their wild ancestors. In addition, DGP were much less attentive to their physical environment. Surprisingly, no behavioral difference was found between WGP-1 and WGP-30. Basal cortisol concentrations did not differ between wild and domestic guinea pigs. Catecholamine concentrations, however, as well as the challenge values of cortisol, were distinctly reduced in the DGP. WGP-1 and WGP-30 did not differ with respect to their endocrine stress responses. In the exploration apparatus both forms of wild cavies were much more explorative than the domestic animals. These data suggest that the long-term breeding and rearing of wild guinea pigs in captivity do not result in significant changes in behavior and hormonal stress responses. It appears to take much longer periods of time and artificial selection by humans to bring about characters of domestication in wild animals.

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The history of humankind has been attended by domestic animals for thousands of years. Furthermore, most animals living under human control are domesticated. They were derived from wild animals by a gradual transformation process, called domestication, over many generations and centuries (Fox, 1978; Herre and Röhrs, 1990; Nachtsheim and Stengel, 1977). During domestication, originally wild animals have to adapt to their new conditions in captivity and human care, resulting in long-term genetic changes, to at last become domestic animals (Herre and Röhrs, 1990; Ratner and Boice, 1975). Thus, the deciding characteristic of domestication is the condition wherein the breeding, care, and feeding of animals are controlled by humans over a period of generations (Clutton-Brock, 1989; Darwin, 1859,

1868; Hale, 1969; Price, 1984; Price and King, 1968). Domestication, therefore, involves an evolutionary process based on the shift in selective pressures: with removal of organisms from some natural selection pressures to new natural selection by artificial environments and artificial selection by humans (Boice, 1973; Fox, 1968; Haase, 1980; Price, 1984; Ratner and Boice, 1975). This process is always accompanied by distinct changes in morphology, physiology, and behavior (Clutton-Brock, 1989; Darwin, 1859, 1868; Fox, 1978; Hale, 1969; Herre, 1981; Herre and Röhrs, 1990; Price, 1984; Sachser, 2001).

In the domesticated form, a distinct increase in the variability of some characteristics (e.g., body size, color) is brought about (Clutton-Brock, 1989; Darwin, 1868; Herre, 1981; Herre and Röhrs, 1990; Price, 1984); on the other hand, a conspicuous convergence of characters between the domesticated forms of different species exists (Herre, 1981;

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Herre and Röhrs, 1990) that are designated as domestication characters (Lickliter and Nees, 1990; Nachtsheim and Stengel, 1977). Due to these domestication characters, domestic animals can be distinguished from their ancestors.

Guinea pigs (*Cavia aperea* f. *porcellus*), for example, were domesticated 3000–6000 years ago in the highlands of South America (Hückinghaus, 1961; Herre and Röhrs, 1990). Their wild ancestor, the wild cavy (*Cavia aperea*) is among the most common and widespread rodents of South America (Rood, 1972; Stahnke and Hendrichs, 1988). The domestic guinea pig played an important role in providing the Indians with meat. Today this animal is among the most popular pets and common laboratory animals. The comparison of wild cavies, kept and bred in captivity, with the domestic form, the guinea pig, reveals changes in behavior as well as in hormonal stress responses due to the domestication process (Künzl and Sachser, 1999). In the domestic guinea pig for example, the reactivity of the sympathetic–adrenomedullary (SAM) and the hypothalamic–pituitary–adrenocortical (HPA) systems is markedly reduced compared with their wild counterparts. This reduction in stress responsiveness may constitute a physiological mechanism that helps domesticated animals adjust to human-made housing conditions.

The time frame required for domestication is controversial. Thus, the question arises whether wild animals that were kept and bred for several generations in human-made conditions are still “true” wild animals or whether they are already domesticated. This issue has become increasingly important, since many endangered species have now vanished from their natural habitats and can be found in zoos only. If living in captivity for a few generations alters behavior and endocrine stress responses, then it would be problematic to use these animals for releasing programs.

In this study, we investigated whether wild cavies that were bred and reared under human control for generations show characters of the domestic form or whether they are still “true” wild mammals. For this purpose, we conducted two experiments. First, we compared the spontaneous behavior and endocrine stress responses of adult domestic guinea pigs and two populations of their wild counterparts: one population of the wild cavies consisted of wild-trapped animals and their first laboratory-reared offspring. The animals of the other population were reared in captivity for about 30 generations. Second, we compared the exploratory behavior of the three populations of guinea pigs in a specially designed test apparatus.

Methods

Subjects

The experiments were conducted with the domestic guinea pig (a) as well as two populations of wild cavies (b, c):

- a) The domestic guinea pigs (*Cavia aperea* f. *porcellus*) used (DGP) were descendants of a heterogeneous short-haired and multicolored stock of 40 animals obtained from a breeder in 1975. Through natural markings all domestic guinea pigs were known individually.
- b) One population (WGP-30) of wild guinea pigs (*C. aperea*) consisted of descendants from feral individuals trapped in the wild in the Province of Buenos Aires, Argentina, in 1974. Thus they had been living for about 30 generations under human-made conditions. During this time the animals were bred without goal-directed selection.
- c) The other population (WGP-1) consisted of wild trapped animals from the Province of Buenos Aires, Argentina, as well as of their first laboratory-reared offspring.

All wild cavies were marked by blanching their coat with hydrogen peroxide.

Animal maintenance

All animals were housed under standard conditions: 12:12 L:D cycle, photoperiod 07:00–19:00 h, temperature $20 \pm 2^\circ$ C, relative humidity about 60%. The floors were covered with standard bedding material (wood shavings). Commercial guinea pig diet (Altromin 3022, Altromin Lage and Höveler “Spezialfutter” 1070 for guinea pigs, Höveler Spezialfutterwerke GmbH & Co KG, Langenfeld, Germany), rolled oats, and water were available ad lib. This diet was supplemented regularly with fruits and hay.

Experiment 1

The first experiment was conducted to compare the spontaneous behavior as well as endocrine stress parameters of WGP-30, WGP-1, and DGP. Six groups each of WGP-30 and WGP-1 and nine groups of DGP, each consisting of one adult male and two adult females, were used. The groups were kept in 1.5-m² enclosures. All subjects were adult; that is, they were at least 6 months of age. All females had already given birth. The offspring of these groups remained with their parents until weaning and then were taken out of the enclosures. During the time of experiments no offspring were present and no female was in estrus.

Procedures

The spontaneous behavior of all members in each group (one male, two females) was recorded by videotape five times for 2 h (WGP-1, WGP-30) or 10 times for 2 h (DGP) within a period of 2 weeks, always between 08:00 and 10:30 h; that is, the total observation time amounted to 300 h. In addition, blood samples were taken from all males on 2 different days (Days A and B) in the 2-week observation period to determine serum hormone concentrations. On Day

A, a so-called challenge test was conducted: each male was caught and a blood sample was taken at 13:00 h within a maximum time of 3 min. Cortisol concentrations determined from this sample were designated as initial values. Immediately after the first sample, the individuals were placed into an unfamiliar, clean cage (size 0.5 m²) with food and water available. At 60 and 120 min after collection of the first sample a second and a third sample were taken to determine cortisol concentrations (60- and 120-min challenge values, respectively). Afterward the males were returned to their home cages. One week later (Day B) a further blood sample was taken at 13:00 h (within a maximum time of 5 min) for the determination of catecholamine concentrations: this time, however, only initial values were determined.

Blood sample collection

Blood samples were taken by puncturing the marginal ear veins. In guinea pigs, sampling blood by puncturing the ear vessels is a nonstressful event that does not lead to an increase in cortisol concentrations (Sachser, 1994). Thus, there was no need to anesthetize the animals. It is no more difficult to take blood samples from the wild animals than from the domestic guinea pigs. For example, the wild animals need not be held tighter than the domestic animals during blood sample collection. Therefore, the time required to take samples was not different in wild and domestic animals.

About 100 to 150 μ l blood was taken. From the first samples (initial values) and from the samples taken during the challenge test, serum cortisol concentrations were determined. The blood was collected in heparinized capillaries, separated by centrifugation (11,752g for 5 min), and deep frozen (-20°C) until assayed. From the samples taken 1 week later, serum epinephrine (E) and norepinephrine (NE) concentrations were determined. The blood was collected in iced heparinized capillaries, separated by centrifugation, deproteinized (6 N perchlorid acid), and stored at -20°C until assayed.

Hormone determination

Serum concentrations of cortisol were determined in duplicate by radioimmunoassay without chromatography using a specific antibody against cortisol. To each 5- μ l sample volume (serum:phosphatbuffer = 1:2) and standard volume, 200 μ l glutamic acid was added. After incubation for 15 min at 95°C , the samples were cooled and centrifuged (1540g for 5 min). Subsequently the antiserum (Sigma Biosciences, Product No. C-8409) and tritium-labeled cortisol (1,2,6,7-³H, 99.8 Ci/mmol, NEN) were added. The following day, antibody-bound and free cortisol fractions were separated by dextran-coated charcoal. The antiserum used cross-reacted with relevant steroids as follows: cortisol 100%, 17- α -hydroxyprogesterone 12.2%, 11-desoxycortisol 7.2%, desoxycorticosterone 4.8%, corticosterone 4.1%. The intraassay and interassay coefficients of

variation for cortisol were 4.8 and 8.7%, respectively. Further details of assay performance have been published elsewhere (Fenske et al., 1982; Fenske and Probst, 1982).

Serum concentrations of E and NE were determined by radioenzymatic assay (Da Prada and Zürcher, 1976). E and NE were converted into their [³H]methoxy derivates by incubation with *S*-adenosyl-L-[methyl-³H]methionine (55–85 Ci/mmol; NEN) in the presence of catechol-*O*-methyltransferase. Labeled products were isolated by organic extraction and thin-layer chromatography. The intraassay coefficients of variations were 7% for N and 6% for E.

Behavioral measures

The categorization of behavioral patterns has been described previously (Kunkel and Kunkel, 1964; Rood, 1972; Künzl and Sachser, 1999). The following behavioral elements were recorded (sampling rule: focal animal sampling; recording rule: continuous recording; cf. Martin and Bateson, 1993):

Offensive aggressive behavior: head thrust (a jab with the head toward the opponent); attack lunge (a short jump at the opponent); chase; bite.

Sociopositive behavior: social grooming (one animal nibbles another animal's pelage); nudge (one animal pushes another gently with its nose).

Courtship behavior: naso-anal licking (one animal licking, sniffing, or nuzzling another animal's ano-genital region); slink (slow, strained, cowered walking, the head stretching forward, parallel to the ground); rumba [slow approaches of an animal, with rhythmic oscillation of the hindquarters from side to side and emission of a burbling vocalization (the rumble); the head stretching forward, held parallel to the ground, and as the displaying animal nears the female its body may assume a curve].

Orientation behavior: rearing (rearing on the enclosure wall, rearing on an object, rearing without support).

Experiment 2

In a second experiment we investigated the exploratory behavior of male DGP, WGP-30, and WGP-1. The males used for these experiments were kept in all-male groups consisting five or six DGP, WGP-30 and WGP-1, respectively. The exploratory behavior of these animals was assessed in a specially designed exploration apparatus.

Exploration apparatus and test design

At 60–65 days of age, five DGP, six WGP-30, and seven WGP-1 males were tested singly in a test apparatus in which they could explore a novel environment. The test apparatus consisted of a cage (0.25 m \times 0.25 m) and an empty hallway (0.25 m \times 3.80 m). At 18:00 h, the test male was placed into the cage that was separated at that time from the

hallway by a sliding door. At 8:00 h of the following morning the sliding door was opened so that the animal had free access to the unfamiliar environment. In the hallway five photo cells were installed at intervals of 85 cm. The distance between the sliding door and the first photo cell was 20 cm.

Before the beginning of each trial, the apparatus was cleaned with water and wiped out with ethanol. Only the cage was covered with standard bedding material. Food, water, and hay were available ad lib.

Behavioral measures

Two latencies were determined: (1) the time until the male had entered the hallway with all four paws, that is, until the first photo cell was activated; (2) the time until the male had passed completely through the apparatus, that is, until the fifth photo cell was activated. The experiment was stopped if either the animal had passed completely through the apparatus or 9 h had elapsed since the sliding door was opened.

Statistical analysis

Physiological data are presented as means + SEM. Behavioral data of the first experiment are represented as medians and the 10, 25, 75, and 90% quartiles. Behavioral data of the second experiment are presented as medians and individual values. Differences between more than two independent categories were tested with the Kruskal–Wallis one-way analysis of variance (*H* test). In the case of significant variation, post hoc comparisons between two samples were performed using multiple Mann–Whitney *U* tests (two-tailed). Significance levels were corrected by means of the sequential Bonferroni method after Hochberg (Chandler, 1995; Wright, 1992). Differences were considered significant if their probability of occurring by chance was less than 0.05.

Results

Experiment 1

The first experiment was conducted to compare the spontaneous behavior as well as the hormonal stress responses of WGP-30, WGP-1, and DGP.

Behavior

The two populations of wild cavies (WGP-1, WGP-30) did not differ on any of the behavioral elements measured. In contrast, WGP-1 and WGP-30 differed significantly from DGP on most behavioral patterns (Fig. 1). Both male and female DGP displayed more sociopositive behavior (social grooming, nudge) than did WGP-1 and WGP-30. Male DGP displayed significantly more courtship behavior (nasal licking, slink, rumba) and less aggressive behavior

(head thrust, attack lunge, chase, bite) and orientation behavior (rearing) than did WGP-1 and WGP-30. Female DGP showed significantly less aggressive behavior than female WGP-1, though female DGP did not differ from the female WGP-30 with respect to this behavior.

Endocrine stress responses

HPA system. Male wild and domestic guinea pigs did not differ in their initial serum cortisol concentrations. Sixty and 120 min after the animals had been placed into an unfamiliar cage, however, cortisol values were distinctly higher in both forms of wild cavies than in the domestic guinea pigs (Fig. 2). WGP-1 and WGP-30 did not differ in their stress responses.

SAM system. Wild cavies responded in a much more robust fashion to the blood sampling procedure than did the domesticated animals: serum E and NE concentrations were higher in both populations of wild guinea pigs than in domestic individuals, though a significant difference was found only between WGP-30 and DGP (Fig. 3). WGP-1 and WGP-30 did not differ in their catecholamine concentrations.

Experiment 2

In the second experiment, we investigated the exploratory behavior of male DGP, WGP-30, and WGP-1. All wild cavies entered the unknown hallway within a few minutes and passed through it completely within a maximum time of 44 min. In striking contrast, only a single domestic guinea pig entered the hallway more than 1 h after the sliding door was opened, and none of the DGP passed through it completely within the 9-h testing period. WGP-1 and WGP-30 did not differ in their latencies (Fig. 4).

Discussion

The results show clearly that the domestication process led to distinct differences in behavior and hormonal stress responses of domestic and wild animals. Interestingly, wild animals living for 30 generations in human-made conditions (WGP-30) did not differ from wild-trapped animals and their first laboratory-reared offspring (WGP-1). One could argue that no difference existed between WGP-30 and WGP-1 because WGP-1 consisted of individuals trapped in the wild as well as of individuals that were born in the laboratory. This explanation, however, seems rather unlikely: almost all behavioral frequencies and hormone concentrations of wild-trapped animals were within the same range as those of their first laboratory-reared offspring.

Experiment 1

Domestic guinea pigs and their wild ancestors differed with respect to aggressive, sociopositive, male courtship,

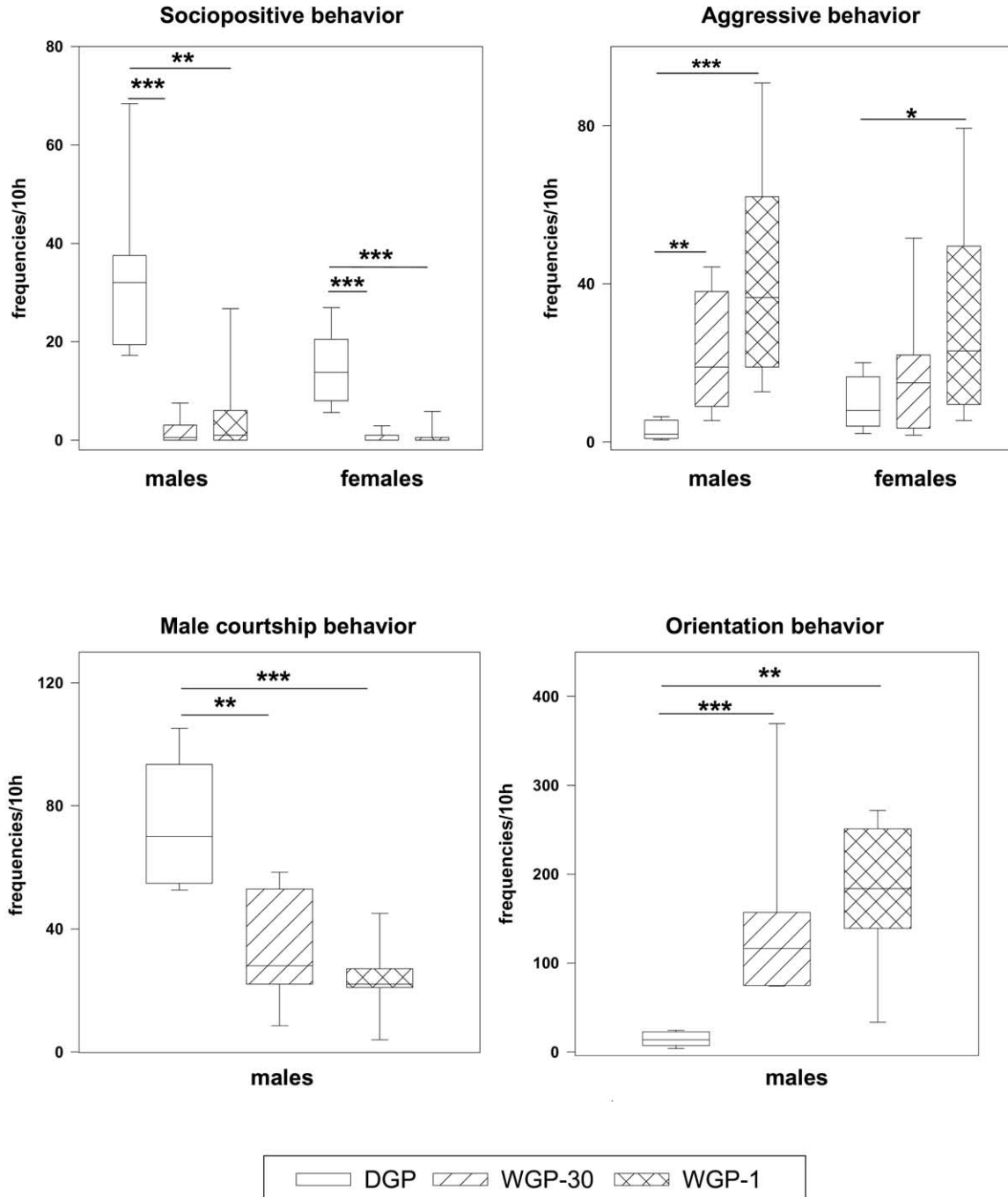


Fig. 1. Frequencies of behavioral patterns in wild and domestic guinea pigs. Offensive aggressive behaviors (sum of head-thrust, attack-lunge, chase, and bite), sociopositive behaviors (sum of social-grooming and nudge), male courtship behaviors (sum of naso-anal licking, slink, and rumba), and orientation behaviors (sum of rearing on the enclosure wall, rearing on an object, rearing without support). Values are given as medians and the 10, 25, 75, and 90% quartiles. DGP, domestic guinea pigs; WGP-30, wild guinea pigs, living for 30 generations under human-made conditions; WGP-1, wild-trapped wild guinea pigs and their first laboratory-reared offspring. Statistics: H test with subsequent Mann–Whitney U tests (two-tailed), adjusted with the sequential Bonferroni method. Aggressive behavior males: $H(2) = 13.9, P < 0.001$; aggressive behavior females: $H(2) = 6.2, P < 0.05$; sociopositive behavior males: $H(2) = 13.0, P < 0.001$; sociopositive behavior females: $H(2) = 28.7, P < 0.001$; male courtship behavior: $H(2) = 13.4, P < 0.001$; rearing: $H(2) = 13.9, P < 0.001$. $N = 9$ (DGP males), $N = 18$ (DGP females), $N = 6$ (WGP-30 and WGP-1 males), $N = 12$ (WGP-1 and WGP-30 females). ** $P < 0.01$, *** $P < 0.001$. Horizontal bars indicate post hoc tests only.

and orientation behavior. These findings agree with those of earlier studies on the same species by Rood (1972), Stahnke (1987), and Künzl and Sachser (1999): the process of do-

mestication in guinea pigs has led to typical traits—reduced aggressiveness, increased tolerance of conspecifics—that have also been found in comparisons between wild and

domestic forms of other species (e.g., rats: Boice, 1972; Barnett from Boreman and Price, 1972; Barnett and Stodart from Fox, 1978; Richter, 1954; cats: Zimmermann from Hemmer, 1983; mallard ducks: Desforges and Wood-Gush from Haase, 1980). In addition, the wild cavies displayed significantly less courtship behavior than did domestic guinea pigs. This striking difference might indicate a lower threshold for the display of courtship behavior in the domestic guinea pig, a trait that is also regarded as a characteristic of domestication (Hemmer, 1983; Herre and Röhrs, 1990; Price, 1984).

The higher frequencies of rearing that were displayed by the wild cavies indicate that these animals were much more attentive to the surrounding of their enclosures than were the domestic guinea pigs. This finding agrees with data from other species: wild forms of rats (Huck and Price, 1975), dogs (Herre, 1981), pigs (Kruska and Röhrs from Hemmer,

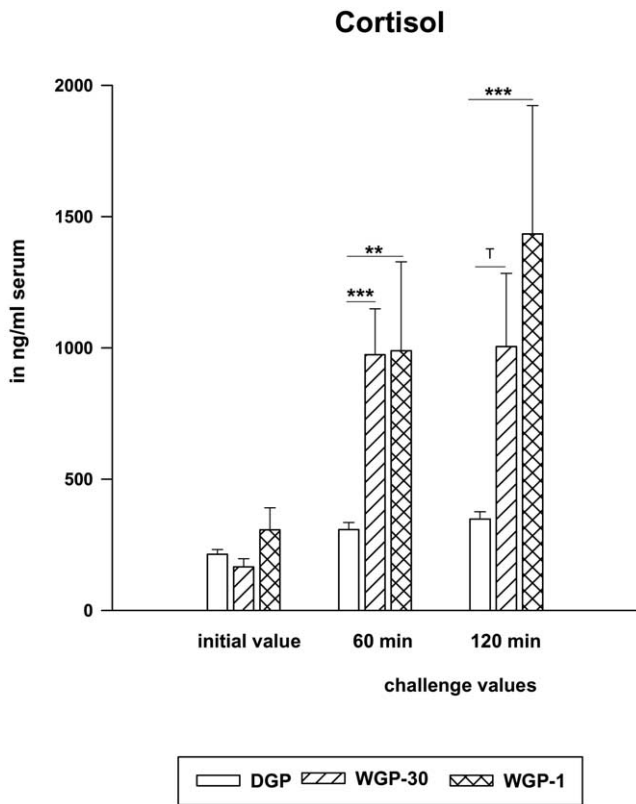


Fig. 2. Serum cortisol concentrations in male wild and domestic guinea pigs. Values are given as means and SEM. DGP, domestic guinea pigs; WGP-30, wild guinea pigs, living for 30 generations under man-made conditions; WGP-1, wild-trapped wild guinea pigs and their first laboratory-reared offspring. Initial values: concentrations before the males were placed singly into an unfamiliar cage; 60- and 120-min challenge values: concentrations determined 60 and 120 min after taking the initial value. Statistics: *H* test with subsequent Mann–Whitney *U* tests (two-tailed) adjusted with the sequential Bonferroni method. Initial values: $H(2) = 0.58$, n.s.; 60-min challenge values: $H(2) = 14.2$, $P < 0.001$; 120-min challenge values: $H(2) = 10.9$, $P < 0.01$. $N = 9$ (DGP) and $N = 6$ (WGP-1, WGP-30), respectively. $T = 0.05 < P < 0.1$. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Horizontal bars indicate post hoc tests only.

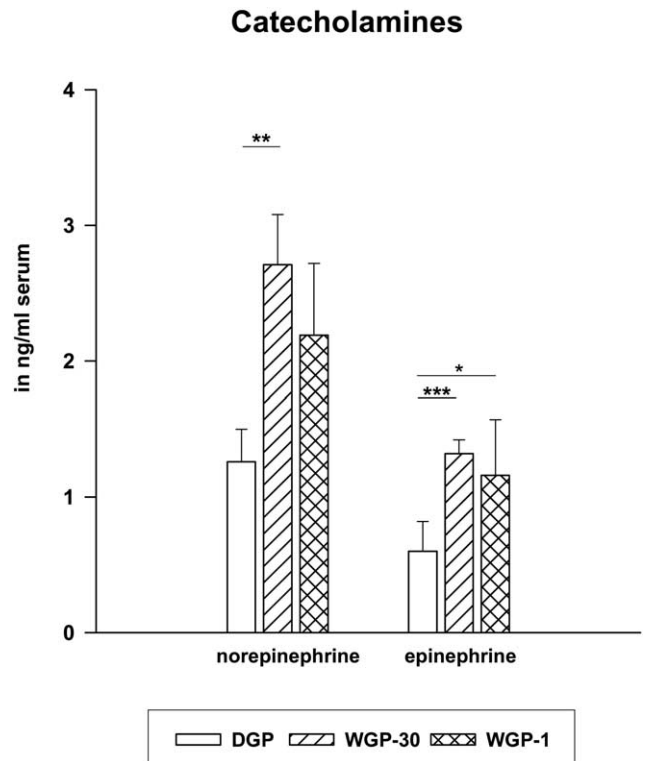


Fig. 3. Serum epinephrine and norepinephrine concentrations in male wild and domestic guinea pigs. Values are given as means and SEM. DGP, domestic guinea pigs; WGP-30, wild guinea pigs, living for 30 generations under man-made conditions; WGP-1, wild-trapped wild guinea pigs and their first laboratory-reared offspring. Statistics: *H* test with subsequent Mann–Whitney *U* tests (two-tailed) adjusted with the sequential Bonferroni method. Epinephrine: $H(2) = 11.9$, $P < 0.01$; norepinephrine: $H(2) = 7.2$, $P < 0.05$. $N = 9$ (DGP) and $N = 6$ (WGP-1, WGP-30), respectively. $T = 0.05 < P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Horizontal bars indicate post hoc tests only.

1983), and ducks (Cheng et al., 1979; Desforges and Wood-Gush, 1975 from Haase, 1980) also direct greater attention to the environment than do their domestic counterparts. This reduction of alertness and sensitivity to environmental change is a further trait typical of domesticated animals (Herre, 1981; Price, 1984). This is not surprising since a selection against overactive and nervous animals exists during domestication, and sensitivity confers no obvious selective advantage in captivity (Gottlieb, 1961; Price, 1973).

We found differences between domesticated and wild animals not only in their behavior, but also in their reactivity of the endocrine stress systems. The HPA and SAM systems play a major role in adjusting an individual to its physical and social environment. The activation of each of these systems provides the organism with energy and shifts it into a state of heightened reactivity that is a prerequisite for responding to environmental changes in an appropriate way. Since domestic and wild animals live in completely different environments, it can be expected that changes in the activity and reactivity of the organism's stress axes have occurred during the process of domestication.

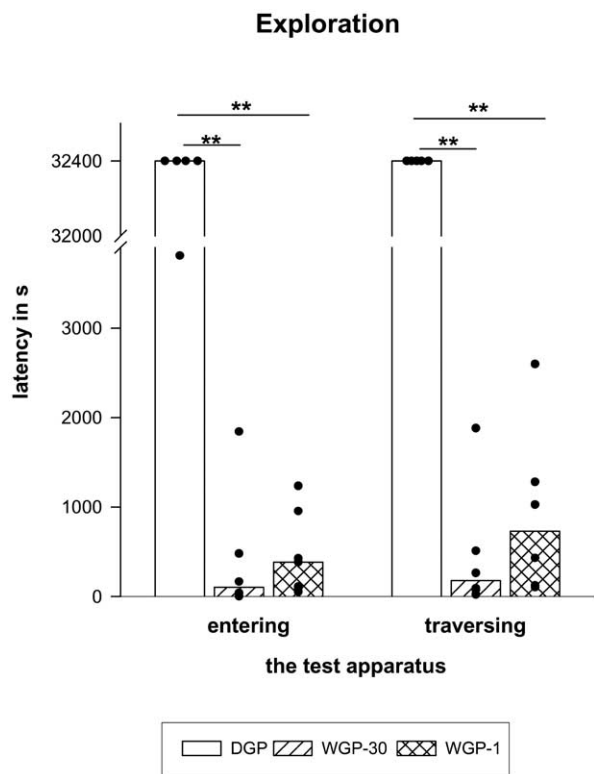


Fig. 4. Time in seconds until the animals first entered and first completely traversed the test apparatus, respectively, for male domestic and wild guinea pigs. The experiment was stopped if either the animal had passed completely through the apparatus or 9 h (=32,400 s) had elapsed after initiation of the experiment. Values are given as medians and individual values. DGP, domestic guinea pigs; WGP-30, wild guinea pigs, living for 30 generations under human-made conditions; WGP-1, wild-trapped wild guinea pigs and their first laboratory-reared offspring. Statistics: H test with subsequent Mann–Whitney U tests (two-tailed) adjusted with the sequential Bonferroni method. Entering: $H(2) = 10.8$, $P < 0.01$; passing through: $H(2) = 11.1$, $P < 0.01$. $N(\text{DGP}) = 5$, $N(\text{WGP-1}) = 7$, $N(\text{WGP-30}) = 6$. $^{**}P < 0.01$. Horizontal bars indicate post hoc tests only.

In the present study, serum cortisol concentrations were determined from blood samples taken within 3 min of entering the animals' housing room (initial values). Thereafter, the animal was transferred to a clean, unfamiliar cage, and a second and third sample were taken 60 and 120 min later (challenge values). In caviomorph rodents, glucocorticoid concentrations do not change within a time span of 5 min in response to a stressor (guinea pig: Sachser, 1994; yellow-toothed cavy, a South-American rodent belonging to the same subfamily as *C. aperea*: Schwarz-Weig, 1998). Therefore, the initial values represent reliable indications of the animals' basal HPA activity. In contrast, the challenge values give information about the HPA reactivity to a combination of stressors including catching and handling the animals, taking a blood sample, and exposing them to a novel environment. In agreement with a former study (Künzl and Sachser, 1999), the basal HPA activity was not different between domestic guinea pigs and wild cavies. The reactivity of this stress axis, however, was distinctly higher

in the wild ancestor. The cortisol concentrations of WGP-30 and WGP-1 did not differ. A higher reactivity of the HPA system in domesticated animals compared with their wild counterparts is also found in mallards and mice (Martin, 1978). Furthermore, the duration of the corticosterone response to immobilization stress is longer in wild than in domestic ducks (Martin, 1978). Thus, good evidence exists that the process of domestication has led to a reduced responsiveness of the HPA system in all species studied so far. Whether or not the basal activity of the HPA system is also lower in the domesticated form might be species-dependent.

Serum catecholamine concentrations in wild and domestic guinea pigs were determined to assess the responsiveness of the SAM system. The concentrations of E and NE reflect the responsiveness of this system to the blood sampling procedure, as in small animals basal values of these hormones can be obtained only by indwelling catheters and in the absence of handling, which is not feasible in small and highly active animals living in social groups (Bühler et al., 1978; Sachser, 1987). Our data revealed a marked reduction in the concentrations of E and NE in the domestic animals compared with their wild counterparts, similar to results of Künzl and Sachser (1999). The reduced reactivity of the SAM system might be the physiological correlate of the reduced alertness, nervousness, and sensitivity of the domesticated animals compared with their wild counterparts. While this trait appears to help domestic animals adapt to human-made housing conditions, it is counter selected in wild animals in their natural habitats by natural selection. The reduced responsiveness of the HPA as well as the SAM system probably enables animals to cope with artificial environments. Interestingly there was no difference between wild animals living for 30 generations in human-made conditions (WGP-30) and wild-trapped animals and their first laboratory-reared offspring (WGP-1). Thus living for 30 generations in artificial environments per se did not lead to such adaptations. A goal-directed artificial selection might be necessary to bring about these effects.

Experiment 2

In the second experiment, we compared the exploratory behavior of male domestic guinea pigs and males of both populations of wild cavies: DGP were much less explorative than WGP-30 and WGP-1. The two populations of wild guinea pigs, however, did not differ.

Some points have to be taken into account when exploratory behavior is measured. For example, fear inhibits exploratory behavior in novel situations (Blanchard et al., 1974; Russell, 1973). Thus, the increased level of exploration results from the interaction of curiosity and fear (Aitken, 1974; Grandin and Deesing, 1998). In an open field, for example, the animals have no possibilities for retreat. Such an exploration is designated as "forced exploration" (Blanchard et al., 1974; Goodrick, 1974). It is assumed that

domestic and wild animals behave in forced situations (e.g., open fields) differently due to different degrees of fear (Smith, 1972). This results in different amounts of exploration. Such “forced exploration” can be very different from exploratory behavior shown by animals who have the opportunity to retreat. This “free exploration” can be investigated in a test apparatus where the new environment that is to be explored is attached to the home cage, as was the case in our test situation (e.g., Blanchard et al., 1974; Osborne, 1977; Wood-Gush and Vestergaard, 1991).

The domestic guinea pigs explored much less than the wild animals. The reduction of the exploratory behavior was so dramatic that most domestic guinea pigs did not even enter the unfamiliar environment within 9 h, whereas all wild guinea pigs (WGP-30 and WGP-1) explored it completely within a maximum time of 44 min. This finding corresponds to the higher frequencies of rearing in wild cavies found in the first experiment, indicating that these animals directed greater attention to their environment. The higher SAM activation in wild cavies might have driven their more intensive exploratory behavior.

The decline in exploration seems to be a general character of domestication that is also found in dogs, rats, and mice (Barnett and Smart, 1975; Frank and Frank, 1982). In wild animals, exploratory behavior is crucial for surviving in their natural habitat (Baum, 1994; Wood-Gush and Vestergaard, 1991). In contrast, under human control there is no need for extensive exploratory behavior. Interestingly, our data show that it again requires more than a few generations to bring about this domestication trait.

Conclusions and general implications

Only a few studies have addressed the question of whether or not domestication characters occur in wild animals that are kept and reared under artificial conditions. Wild house mice, for example, do not differ with respect to their behavior from conspecifics, which have lived in laboratories for 10 years. However, the behavior of both populations is very different from that of domesticated laboratory mice (Conner, after Price, 1984). In contrast, deermice that have been bred for 25 generations in captivity are less cautious than their wild counterparts when they are exposed to foreign objects (Price, 1979). Our study investigated both physiological and behavioral parameters. To summarize, wild and domestic guinea pigs showed distinct differences in behavior and endocrine stress responses, whereas the two different populations of wild cavies did not differ on any of the behavioral or hormonal parameters measured.

What are the general implications of this study? At first view it seems astonishing that housing wild animals for 30 generations under artificial conditions did not lead to any changes in endocrine stress responses and behavior, particularly since important natural selection pressures no longer impinged on the individuals under human housing condi-

tions. This finding draws attention to the important effects of sexual selection. In natural populations, male–male competition and female choice usually result in extreme variation in lifetime reproductive success of the animals, that is, a few individuals will pass on their genes at a disproportional large amount, while a large number of individuals will not contribute to the gene pool of the next generation at all (Alcock, 1998; Trivers, 1985). Under our housing conditions, we artificially excluded the influence of sexual selection, that is, we paired the animals by chance. Hereby we obviously preserved the genetic diversity of the founder animals and, as a consequence, no domestication characters occurred in either stress responses or behavior. Correspondingly, much larger animal numbers are required to preserve a comparable amount of genetic diversity in natural populations due to the effects of sexual selection. This insight has optimistic implications for conservation biology. Keeping relatively small populations of (endangered) wild mammals in zoos for generations does not necessarily mean that these animals will develop characters of domestication and therefore will no longer be suitable for releasing programs. As our study shows convincingly, wild guinea pigs reared and kept under artificial conditions for about 30 generations are still “true” wild mammals.

On the other hand, selective breeding of wild animals from the extremes of a behavioral continuum can bring about distinct differences between lines of animals within a very short time. When mink, for example, are selected for fearful or confident reactions toward humans it takes no more than 10 generations for nonoverlapping populations to develop with respect to this trait (Malmquist and Hansen, 2001). Hence, changes in selection pressure can change the frequencies of specific types of behavioral responses dramatically within a rather short time. It would be worthwhile to conduct similar experiments with wild guinea pigs to elucidate the time scale required to bring out characters of domestication by selective breeding.

In general, domestic animals are more tolerant and less aggressive toward conspecifics than their wild counterparts. As a consequence, social processes proceed in a completely different way. When domestic guinea pigs are kept in breeding groups of one adult male and several adult females, the mature sons and daughters will integrate rather peacefully into the social system of the groups and all animals will cohabitate in a nonaggressive and nonstressful way (Sachser, 1998). When adult wild cavies are kept in breeding groups of one male and several females, a completely different picture emerges: the daughters integrate into the linear dominance hierarchy of the females. In contrast, the father and his sons become rather incompatible when the sons attain sexual maturity. Then, in most cases, the sons must be taken out of the groups or the father will injure or even kill them (Sachser, 1998). These differences in behavior may be due mainly to different temperaments of wild and domestic animals, in particular, a reduced alertness, nervousness, and sensitivity of the domestic animals. From

our endocrinological data we argue that these traits are causally related to a reduction in the reactivity of the organism's stress axes. If so, solely the reduction of SAM and/or HPA reactivity would bring about changes in social behavior, social interaction patterns, and social organization. Such changes in endocrine reactivity would not require extensive changes at the genomic level. In contrast, even a point mutation causing a change in the control systems of endocrine reactivity would have the potential to generate changes in temperament and, subsequently, in the course of social processes. Therefore, a change in selection pressures might lead to distinct changes in social organization within a few generations by acting on the animals' control systems for endocrine reactivity.

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