Associations between first encounters and ensuing social relations within dyads of two species of lacertid lizards

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Researchers often presume that dominant individuals, during an initial series of social interactions, ultimately gain possession of the territory, but detailed studies of the process of social relation establishment in animals are rare. We used an experimental approach on pairs of conspecific newborns of two lizard species (*Podarcis sicula* and *P. melisellensis*) to examine whether the outcomes of first encounters are consistent with the formation of social relations during the ensuing three weeks. A major objective was to determine whether social relations expressed during prolonged cohabitation induced divergence of individual growth rates within a dyad. Moreover, we explored to what extent individual differences in growth rate and behavior during social cohabitation paralleled differences expressed when the animals were housed in isolation. Differential expression of behavior within dyads was examined by calculating the difference between values for the two individual lizards. During brief first encounters, access to a localized basking site was determined by agonistic interactions between lizards. Cohabitation of two lizards during prolonged encounters resulted in differences in their thermal microhabitat usage, which in turn induced divergence of their growth rates. The direction and magnitude of the differences in thermal microhabitat use and the divergence in growth rates during prolonged encounters mirrored differences in the interactions exhibited during the first encounter. Moreover, differences between two lizards in initial social interactions, and in thermal microhabitat use and growth rate during prolonged encounters, paralleled differences in thermal microhabitat use exhibited when lizards were housed alone. Thus, it may be possible to predict the outcome of social interactions within dyads based on the differential expression of traits between two lizards housed in isolation. *Key words:* social relations, first interactions, growth, thermal habitat use. *[Behav Ecol 15:938–945 (2004)]*

Comprehensive literature on factors affecting the nature and outcome of social interactions in territorial species exists (reviewed in Cloutier and Newberry, 2000; Martin et al., 1997; Stamps and Krishnan, 1995), but we know little about how social relations are established in the first place. In theory, first social encounters determine the stable spatial and social relationships that are typical of animals living in established territorial neighborhoods (Beaugrand, 1997; Grafen, 1987; Maynard Smith, 1982; Pratte, 1997; Ydenberg et al., 2001). This rationale forms the basis of many empirical studies of territorial animals. Researchers presume that dominant individuals, during an initial series of social interactions, ultimately gain possession of the territory (for examples see Krebs, 1982; Peeke et al., 1995). However, detailed studies of the process of social relation establishment in animals are rare (Beaugrand and Beaugrand, 1991; Cloutier and Newberry, 2000; Stamps, 1995; Stutchbury, 1991), and most information on this issue is anecdotal or indirect (for notable exceptions see Baker and Aureli, 2000; Stamps and Krishnan, 1994a,b).

Social status may have significant implications for the expression of life history traits (but see Dewsbury, 1982). For example, studies on a range of taxa demonstrate that even under food ad lib conditions, individuals living within the same patch of microhabitat often have different growth rates (Metcalfe et al., 1992; Stamps, 1984b; Stamps and Eason, 1989; Stamps and Tanaka, 1981a,b). Laboratory experiments suggest

that social factors may be responsible for some of this variance; when food abundance, distributions, and other factors are controlled, high status individuals tend to grow faster than low status individuals (e.g., Metcalfe et al., 1992; Stamps, 1984a,b). This variation in early growth rate can be important in determining subsequent life-history patterns. In some species, for instance, individuals that attain a threshold growth rate early in life will mature and reproduce sooner than slower-growing individuals of similar age (Metcalfe et al., 1992; Metcalfe and Monaghan, 2001; see also Downes, 2001; Skelly and Werner, 1990). Thus, individuals that grow slowly early in life, as a consequence of social avoidance, may experience lower reproductive success. However, to understand how social status affects life-history traits it is necessary to know whether animals establish predictable social relations after meeting for the first time.

Herein we describe one of the first controlled laboratory studies designed to examine to what extent the outcome and intensity of interactions between two individuals during their first encounter predicted their social relations during the ensuing period of cohabitation. A major additional objective was to determine whether social relations expressed during prolonged cohabitation induced divergence of individual growth rates within a dyad. Moreover, we explored to what extent individual differences in growth rate and behavior during social cohabitation paralleled differences expressed when the animals were housed in isolation. Our study animals were socially naïve hatchlings of two species of lacertid lizards (*Podarcis sicula* and *P. melisellensis*) with highly similar ecology and social behavior. We reared lizards individually during an initial period and then staged first encounters between pairs of size-matched conspecific lizards and scored aggression as they interacted for access to a localized heat resource. The

same lizard pairs cohabited during the ensuing three weeks, and we estimated the difference in resource use and growth in body size between members of a dyad.

The setup of our experiments required lizards to interact for access to a restricted basking site. *P. sicula* and *P. melisellensis* regularly bask to regulate their body temperature (Avery, 1984; Grbac and Bauwens, 2001; Van Damme et al., 1990). The importance of accurate thermoregulation follows from the direct effects of body temperature on the rate of biochemical and physiological processes, which in turn affect whole-animal performance abilities, and hence fitness (Huey, 1982; Huey and Kingsolver, 1989; Huey and Stevenson, 1979; Van Damme et al., 1991). Thus, access to a basking spot can be considered as similar to the acquisition of a resource and has cascading effects on a suite of performance capacities.

METHODS

Study system

Our study species were the European lacertid lizards *Podarcis sicula* and *P. melisellensis*. Adults of both species display the same stereotypical behavior during interactions with conspecifics and are highly territorial (Nevo et al., 1972; Raynor, 1989). However, very little is known about the social behavior of juveniles in these or other species of lacertid lizards. The two species have similar preferred body temperatures (i.e., ~32°C–36°C; Bauwens and Downes, unpublished data) and thermoregulate by basking on small rocks and stone walls (sometimes in small sun flecks) and by shuttling between sunlit and shaded microhabitats (Avery, 1984; Grbac and Bauwens, 2000; Van Damme et al., 1990).

The data presented herein were collected while investigating competition between *P. sicula* and *P. melisellensis* (Downes and Bauwens, 2002). Given that these species have highly similar thermal ecology and social behavior, in the present study we expected analyses to reveal similar patterns. We therefore report data for two species not to contrast their behavior, but rather with the expectation that we could combine data from *P. sicula* and *P. melisellensis* to increase the power of our statistical analyses.

Our study subjects were 6-week old hatchlings of female lizards collected from Croatia in April 2000. *P. sicula* was caught near Novigrad (45° 19′ N, 13° 33′ E) on the Adriatic coast. *P. melisellensis* was collected near Beli (45° 06′ N, 14° 21′ E) on the large island of Cres (~400 km², Northern Adriatic). Animals were transported to and housed at the Institute of Nature Conservation (Brussels, Belgium).

Animal maintenance

Female lizards were maintained in sand-filled terraria (100 × 40 × 40 cm) containing leaf litter and rock shelters. When a lizard oviposited, her eggs were placed individually into 140 ml jars containing vermiculite (−200 kPa). As part of another study, eggs from a clutch were distributed evenly between incubators set at 26 ± 4°C and 28 ± 4°C. Incubators were checked twice daily for hatchling lizards.

Newborn lizards were measured (snout-vent length [SVL]) and placed individually in opaque tubs (20 × 15 × 25 cm) lined with sand and containing shelter. They were housed in a room at 29°C; 60 W fluorescent tubes above the containers provided thermoregulatory opportunities from 0800 until 1800 h. We identified the sex of the lizards when they were 6 weeks old by inspecting the shape of the femoral pores. This method is highly reliable for the species studied (Bauwens, unpublished data).

During maintenance and experimentation, lizards had access to domestic crickets (*Acheta domestica*) and water ad libitum, both of which were supplemented with calcium and

vitamins, and the light cycle was that of the external environment (i.e., 14:10 h light:dark).

Experimental procedures

We assessed individual differences in growth and behavior of solitary lizards before staging encounters ("solitary period"). We stress that lizards did not experience social interactions during this 6-week period. We included this solitary period in our design to obtain baseline estimates of individual growth rate and behavior, which were used to evaluate divergence of these traits during the ensuing social encounters. When lizards were 6 weeks old (mean ± SE age: 46.9 ± 0.6 days) we staged encounters between pairs of conspecific lizards of both species. We conducted two complimentary experiments with each pair. The first experiment involved staging interactions over a 20 min period and examining social behavior ("first encounter"). The second experiment involved staging interactions over 21 days and periodically measuring microhabitat use, levels of activity, and body size ("prolonged encounter"). This design allowed us to examine to what extent the outcome and intensity of interactions between two individuals during their first encounter predicted their social relations during the ensuing period of cohabitation.

Experiments were performed in terraria (100 × 40 × 20 cm) lined with sand and covered with leaf litter. A slate retreat-site and a water dish were placed at one end of the arena. One 100 W light globe positioned 30 cm above the substrate acted as a heat source (attaining 55°C) on a limited area at the other end of the arena. We used foil to direct the beam of light onto a small (5 × 2 cm) basking site. The limited area of the basking spot precluded both lizards from basking at the same time unless they were positioned within 4cm of each other. To encourage lizards to utilize this resource, we maintained our experimental room at 24°C, which is considerably lower than the preferred body temperatures of both species. To increase structural complexity in the test cages and delineate sections of different ambient temperature, we placed pairs of cards (10 × 4 cm, positioned 10 cm apart) vertically in the sand base at 20 cm intervals along the length of the terraria. Each section was assigned a relative thermal value that reflects the proximity of its ambient temperature to the preferred body temperature of our study animals (Figure 1).

We staged encounters for 20 pairs of each species. Individual lizards were used in only one pair. Half of the pairs from each species were comprised of two males and the other half of two female lizards. Individuals within pairs of lizards were never from the same litter as pair-mates. Lizards comprising a pair were matched for SVL (to within 1.5 mm, i.e., < 5% of SVL, in all except two pairs, for which the differences were 2 and 3 mm).

Solitary period
Lizards were raised in individual cages from hatching until the age of ~6 weeks. We measured SVL at 3–4 day intervals and used these measurements to calculate growth rate (see below) of individual lizards when reared in isolation.

Five days before experiencing their first encounters, lizards were placed individually into test cages. Lights were switched on between 0900 and 1700 h. Two days after introduction, we quantified levels of activity and locations of single lizards every 15 min from 0800 to 1800 h. Specifically, we scored whether a lizard was hidden versus active, and, if it was active, we noted which section of the arena it occupied. From these measurements we estimated thermal microhabitat usage (see below) of individual lizards when they were housed individually (i.e., in the absence of social interactions).

First encounters

First encounter trials were conducted between 1000 and 1700 h. Behavior was observed from behind a one-way mirror and recorded onto audiotape using a dictaphone. To distinguish individuals, we stuck one or two tags (1 × 1 mm) on the lizards' backs.

First encounters were staged within a 60 cm long section of the heated end of a test cage that was unfamiliar to both individuals in a pair. A removable partition divided this area transversely into two 30-cm long sections such that the heat source fell in equal portions either side of the division. Each lizard from a pair was placed alone in one side of the experimental arena and allowed to acclimate undisturbed for 30 min.

To begin a trial we removed the partition and recorded when two lizards approached to within 4 cm of each other and then when they moved further than 4 cm apart; this was considered to be one interaction. All interactions between lizards were assigned to one of three types and the lizard that initiated the interaction was given an aggression score:

(1) Approach: one lizard moved directly toward the other, with or without showing aggressive displays, and its opponent moved away (aggression score = 1).
(2) Display fights: one lizard approached the other and both individuals exchanged threat displays (a lizard flattened its body laterally, arched its neck, and raised its posture; aggression score = 2).
(3) Attack fights: usually began with threat displays but escalated to one lizard rapidly running directly toward and sometimes biting its opponent (aggression score = 3).

Immediately after the first interaction, we also recorded the duration of basking by each lizard under the heat source until the trial terminated 20 min later. At the completion of their first encounters, lizard pairs were left undisturbed in their test cages; this was the initiation of the prolonged encounters.

Prolonged encounters

Prolonged encounters were conducted within the entire test cage. Each pair of lizards remained in its test cage for the next 21 days. Lights were switched on daily between 0900 and 1700 h. On the day following their introduction, and every 3 days thereafter, we conducted observations on both lizards in a pair. Every 15 min from 0800 to 1800 h we scored whether a lizard was hidden versus active, and, if it was active, we noted which section of the arena it occupied. After the second day of behavioral observations, and at the end of every observation day thereafter, both lizards in a pair were measured (SVL).

Data analysis

Calculation of variables

We calculated growth rates of individual lizards by regressing the logarithm of SVL against the number of days elapsed since birth. Slopes of these regression lines estimate size-specific growth rates (Sinervo and Adolph, 1989), i.e., growth rates relative to the size at the start of the growth interval (units: mm/mm/day = 1/day). Coefficients of determination of regression lines were rarely < 0.90. We opted to estimate growth in SVL rather than mass, because the latter variable is subject to short-term fluctuations, for example, in feeding status. We calculated individual growth rates for the pre-experimental and the prolonged encounter periods separately.

We estimated thermal microhabitat use as the summation of the thermal values for the terraria sections (Figure 1) that the lizard occupied during the 40 consecutive 15-min
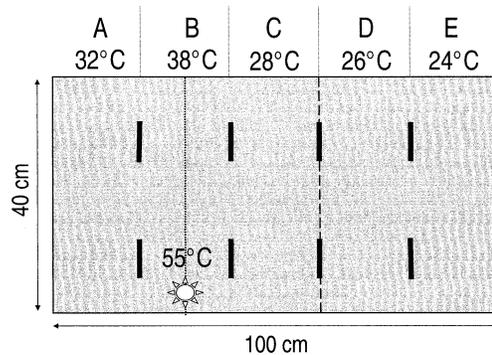
Figure 1
A diagram of the experimental arena showing the positions of the heat bulb and the cards (black bars) that delineated the five thermal sections (A–E; the indicated ambient temperatures were registered using data loggers). The thermal value scores for each section were as follows: area A = 4, area B = 5, area C = 3, area D = 2, and area E = 1. Lizards that were basking under the heat source were assigned a score of 6, whereas hidden lizards received a score of zero. During the first encounters a fixed partition (dashed line) confined the lizards to the left part of the arena; a removable partition (stippled line) divided this area during the initial acclimation phase.

observation periods. The ambient temperatures (as determined using data loggers) attained in each section were: A = 32°C, B = 38°C, C = 28°C, D = 26°C and E = 24°C. The thermal value scores for each section were: area A = 4, area B = 5, area C = 3, area D = 2, and area E = 1. Hidden lizards received a score of zero because they occupied a retreat located in the cold part of the cage, and lizards that were basking under the heat source were assigned a score of 6. Thus, the thermal microhabitat use index is sensitive to the number of observation periods that a lizard was active, i.e., daily duration of activity, and to its proximity to the basking resource. It was calculated for the single observation day during the solitary period and for each of the seven observation days during the prolonged encounter. Preliminary analyses indicated that individual variation in the index of thermal microhabitat usage primarily reflected variation in the daily duration of activity.

For the first encounters, we calculated an individual aggression index as the sum of the aggression scores associated with the interactions initiated by that individual. Thus, the aggression index provides a quantitative estimate for the level of aggression displayed by each individual. During the first encounter trials we directly recorded the duration of basking to estimate the usage of the limited resource by each individual.

Our main objective was to examine to what extent the direction and extent of phenotypic differences between two individuals in a dyad remained constant over the different experimental conditions. To estimate the differential expression of characteristics between paired lizards, we calculated a contrast score for each variable as the difference between the individual values for the two lizards in a pair. Within each lizard pair we arbitrarily decided which individual would have its values deducted from its opponents' values and maintained this same direction of subtraction for all variables. Thus, the sign of the contrast score is arbitrary. High contrast scores, either positive or negative, mean that individuals within a pair exhibited a large difference in the measure, whereas contrast scores close to zero mean that individuals within a pair showed a small difference in the measure.

The behavioral differences between paired lizards during the first encounters were quantified by the contrasts in

Table 1

Descriptive statistics (minimum, 25 percentile, median, 75 percentile, maximum) illustrating variation in the individual values ($n = 80$) and in the absolute values of the contrast scores between paired individuals ($n = 40$) for the characteristics recorded during the three experimental conditions

	Individual values					Contrast score				
	Minimum	25%	Median	75%	Maximum	Minimum	25%	Median	75%	Maximum
Solitary period										
Thermal microhabitat use	6	60	117	166	205	2	15	38	53	152
Size-specific growth rate (day^{-1})	1.32	2.18	2.48	2.71	3.33	0.00	0.25	0.37	0.60	1.01
First encounters										
Aggression score	0	0	1	4	38	0	0	1	8	37
Basking time (s)	0	253	447	721	1200	22	101	218	477	1091
Prolonged encounters										
Thermal microhabitat use: day 1	0	63	100	143	212	2	33	53	93	192
Thermal microhabitat use: days 2 to 7	29	98	134	169	200	−102	−19	20	83	147
Initial SVL (mm)	29.0	32.0	33.8	35.3	38.0	0.0	0.0	0.8	1.0	3.0
Final SVL (mm)	32.0	36.0	38.5	40.5	44.0	0.0	0.5	1.5	2.3	10.0
Size-specific growth rate (day^{-1})	0.88	1.79	2.30	2.85	4.96	0.01	0.30	0.72	1.00	3.62

SVL: snout to vent length; thermal microhabitat use: the sum of the thermal values for the terraria sections occupied by lizards during the experiment; aggression index: the sum of the number of interactions in each of four categories multiplied by a corresponding aggression score.

aggression index, which estimates the asymmetry in aggression levels, and the contrasts in basking time, which quantifies the difference in access to the limited resource. Because these two characteristics were highly correlated (see Results section), we calculated a combined index that integrates both contrast scores. This was obtained by summing the standardized z-values (i.e., mean/SD) for the contrasts in aggression index and basking time, thus giving equal weight to the two composing characteristics.

Statistical analyses

We initially examined variation between species and sexes in the absolute values of the contrast scores for all variables using two-way ANOVA. Analysis of the absolute values of the contrasts is necessary here, as we explore variation in the magnitude of the differences in a dyad for each variable separately. We explored putative differences between species and sexes in the relevant bivariate relationships between contrast variables by comparing slopes and intercepts of the regression equations with ANCOVA. Because we found no significant differences between species and sexes ($p > .10$), neither for the univariate analyses nor for the bivariate relationships, the results reported here are based on a combined data set for both species and sexes.

We calculated correlation coefficients between pairs of contrast variables using regression through the origin. This is a necessary procedure when the sign of the contrast scores is arbitrary (Garland et al., 1992).

RESULTS

Solitary period

Solitary lizards exhibited important individual differences in the index of thermal microhabitat use, almost encompassing the theoretically possible range (0–240; Table 1). Some lizards remained hidden under the retreat (located at the cool end of the cage) during most of the observation day, whereas others spent a large portion of the time active under or near the heat

source. As we did not account for individual differences in thermal microhabitat use in assigning lizards to a pair, the contrast scores for this behavioral trait were highly variable (Table 1). Thus, our staged encounters encompassed lizard pairs whose members exhibited similar microhabitat use during the solitary period (low contrast score) and pairs composed of individuals with highly divergent microhabitat use in the solitary trial (high contrast score).

We also detected important individual differences in growth rate during the solitary period (Table 1), resulting in large differences in SVL at the start of the experimental period (Table 1, listed under "Prolonged encounters—Initial SVL"). Because we matched lizards in a pair for SVL before staging social encounters, contrast scores for growth rate during the solitary period and initial SVL were generally low (Table 1).

First encounters: aggression index and basking time

During their first encounters with a conspecific lizard, 65 out of 80 (81%) individuals engaged in few agonistic behavioral acts and therefore obtained very low aggression indices (0–5; Table 1). Overt aggression ("attack fights") was observed in just four dyads. Absolute values of contrasts for individual aggression indices between paired lizards were low (0–5) in 29 out of 40 (73%) dyads (Table 1). For these pairs, no clear winner and loser could be assigned on the basis of the aggression indices. In 26 out of 29 staged encounters that ended in a draw, the lizards engaged in few (0–5) interactions. Thus, in most of the dyads with a neutral outcome of aggressive interactions, lizards either avoided interacting or were tolerant towards each other, rather than both individuals obtaining high and approximately equal aggression scores.

Individual variation in the time spent basking was highly pronounced and spanned the range bounded by the duration of the trials (0–1200 s; Table 1). Absolute values of contrasts of basking duration were highly variable among dyads (Table 1). Low contrast scores indicate that both individuals basked for approximately equal amounts of time, whereas high scores reveal large differences in basking time between the two
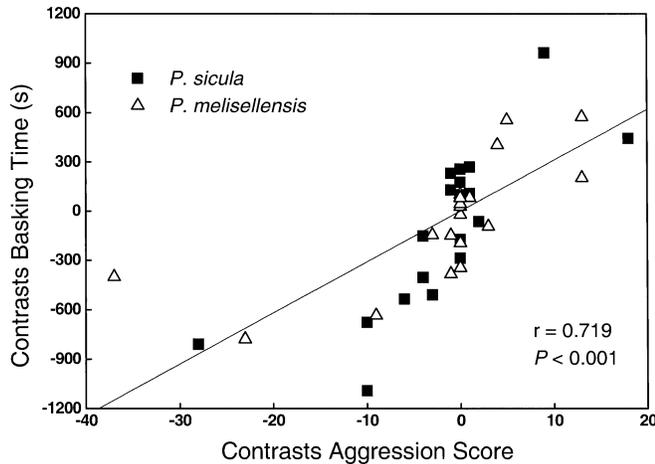
Figure 2
Scatterplot showing correlation between the contrasts for aggression score and the basking time during the first encounters. Each symbol represents the scores for one lizard pair ($n = 20$ for each of both species). The correlation coefficient and regression line were calculated using regression through the origin. The aggression index was calculated as the sum of the number of interactions in each of four categories multiplied by a corresponding aggression score.

Figure 3
Graph showing correlation between the contrast scores for size-specific growth rate and thermal microhabitat use during the prolonged encounters. Each symbol represents the scores for one lizard pair ($n = 20$ for each of both species). The correlation coefficient and regression line were calculated using regression through the origin. Thermal microhabitat use was calculated as the sum of the thermal values for the terraria sections occupied by lizards during the experiment.

members of a pair. In seven dyads, only one of both lizards was observed at the basking spot.

There was a highly significant positive correlation among dyads between the contrasts for aggression index and basking time ($r = .719$, $p < .001$; Figure 2). In dyads with large individual differences in aggression, the most aggressive individual spent much more time basking than its opponent. In pairs that exhibited low contrasts of individual aggression indices, the two individuals either basked side-by-side for approximately equal and considerable amounts of time, or they exhibited clear individual differences in basking time (> 250 s; Figure 2).

Prolonged encounters: thermal microhabitat use

To examine variation in the contrasts during the encounters we used a repeated measures ANOVA model with observation day (1–7) as the within-subjects factor ("time") and "species" and "sex" as between-subjects factors. There were no significant effects of the between-subjects factors and of their interactions with time. However, contrasts of thermal microhabitat use changed significantly with time ($F_{6,216} = 3.12$, $p < .01$). A post-hoc comparison (Newman-Keuls test) identified two homogenous groups: the first observation day, when contrast scores were highest, versus all subsequent (2nd to 7th) days. This decrease over time was primarily induced by changes in the direction (i.e., sign) of the contrast score in some of the experimental pairs after the first observation day. These shifts indicate a reversal between the two individuals in their usage of the thermally most favorable portions of the terraria. We note that all these lizard pairs had low contrast scores during the first observation day, i.e., differences in thermal microhabitat use between the two lizards were small at the start of the encounter. Nevertheless, there was a positive correlation between the scores for the first day and the average score for the subsequent observation days ($r = .599$, $p < .001$) and a high concordance among scores for the separate observation days (Kendall's coefficient of concordance: $W = 0.579$, $p < .001$). These results demonstrate a high consistency within lizard pairs in the relative magnitude of the
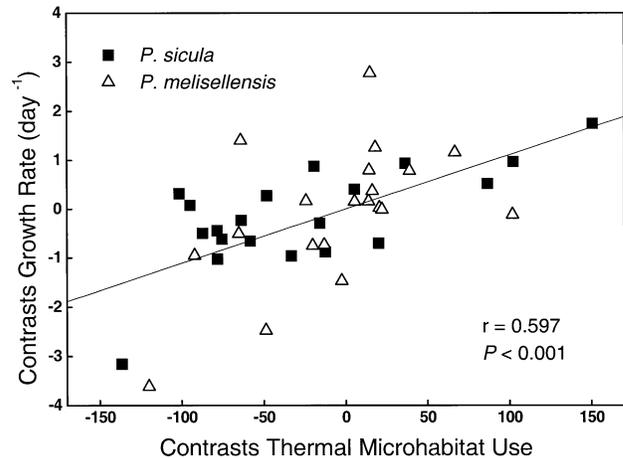
contrast scores throughout the prolonged encounters. Because of this consistency, we opted to use the average value over all observation days as the estimate of thermal microhabitat usage during the prolonged encounters.

Variation in both the individual and the contrast scores for the index of thermal microhabitat usage was high during the prolonged encounters (Table 1). High absolute contrast scores were obtained for dyads in which one lizard was active, and most often exclusively occupied the basking spot, for much longer periods than its opponent. In pairs with low absolute thermal microhabitat use contrast scores, the two lizards were often simultaneously active and they jointly used the basking site.

Prolonged encounters: growth rate

Contrast scores of growth rates during the prolonged encounters were on average higher (paired t test: $t = 3.35$, $p = .002$) and exhibited a much greater variance ($F_{39,39} = 11.79$, $p < .001$) than contrasts in growth rates recorded during the solitary period (Table 1). Contrasts of growth rates during the prolonged encounters and in the solitary period were not significantly correlated ($r = -.263$, $p > .10$). Thus, cohabitation of two lizards during the prolonged encounters resulted in an increased divergence of their growth rates, and these increased differences were not a continuation of divergences that existed when they were housed alone.

During the prolonged encounters the contrast scores for growth rate and thermal microhabitat use were positively correlated among dyads ($r = .597$, $p < .001$; Figure 3). Hence, differences in growth rate between paired lizards mirrored differences in thermal microhabitat usage when they cohabited during the prolonged encounters.

Relationship between solitary period, first encounters, and prolonged encounters

The combined index for behavior during the first encounters was positively correlated with both the contrasts in thermal microhabitat use ($r = .446$, $p = .003$) and the contrasts in
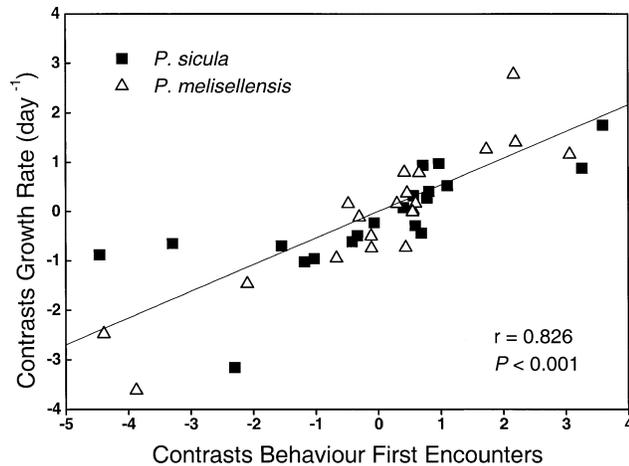
Figure 4
Graph showing correlation between the contrasts for size-specific growth rate during the prolonged encounters and the combined index for behavior during the first encounters. Each symbol represents the scores for one lizard pair ($n = 20$ for each of both species). The correlation coefficient and regression line were calculated using regression through the origin. The combined index for behavior was obtained by summing the standardized z-scores for the contrasts in basking time and in aggression index.

growth rate during the prolonged encounters ($r = .826$, $p < .001$; Figure 4). In other words, dyads in which one lizard was clearly more aggressive and/or basked longer than its opponent during their first encounter subsequently showed the largest differences in thermal microhabitat use and growth rate. Importantly, it was the initially most aggressive individual that spent more time in the thermally most favorable portions of the terrarium and that grew faster. Furthermore, in pairs in which both lizards were equally aggressive and/or basked for approximately equal amounts of time during the first encounters, between-individual differences in thermal microhabitat usage and growth rate during the prolonged encounters were also relatively low.

Contrast scores of thermal microhabitat use during the solitary period were positively correlated with the combined index for the first encounters ($r = .452$, $p = .003$) and with the contrast scores of both thermal microhabitat use ($r = .515$, $p < .001$) and growth rate during the prolonged encounters ($r = .436$, $p = .004$). Thus, differences in thermal microhabitat use between members of a dyad that were evident when they were housed individually predicted differences in social interactions, thermal microhabitat use, and growth rate during the ensuing period of cohabitation.

DISCUSSION

Our staged trials between pairs of conspecific *Podarcis sicula* and *P. melisellensis* revealed three main findings. First, lizards interacted quickly during their first encounters, and the outcome of these interactions predicted the direction and intensity of social relations (as indexed by thermal microhabitat use) during the ensuing three-week period. Second, these social relations induce divergence in growth rates within pairs. A third and unexpected finding is that the outcome of first social encounters within a pair, as well as the divergence in thermal microhabitat use and growth rates during longer periods of cohabitation, were predicted by differences between the paired individuals in thermal microhabitat use while housed in isolation.

In the majority of our experimental dyads, lizards displayed few aggressive interactions and rarely engaged in overt fights during their first encounters. Nevertheless, differences between paired individuals in basking time were often considerable and their sign and magnitude paralleled those of the contrasts in aggression index. Thus, in pairs with a clear outcome of aggressive interactions, it was invariably the most aggressive lizard that spent more time basking than its opponent. This result indicates that precedence of access to the basking site was determined by the outcome of agonistic interactions. In pairs that exhibited low contrasts of aggression indices, between-individual differences in the time spent basking were generally lower. In some of these dyads, the two lizards basked alongside for considerable amounts of time, indicating that they were highly tolerant to each other. However, other pairs that engaged in few aggressive interactions demonstrated clear individual differences in basking time, suggesting that access to the basking spot was determined by subtle behavioral interactions. Overall, our observations show that social relations were established quickly, as soon as two animals completed their first social interaction (see also Stamps and Krishnan, 1994a, and references within). However, dyads differed clearly in the rate and intensity of interactions, ranging from apparent tolerance to clear dominance. This was an unexpected result, as we staged encounters between pairs that were matched for body size in an arena that was unfamiliar to both lizards and we used socially naive animals. This setup was expected to intensify social interactions, as other studies have shown that aggressive interactions tend to be more frequent and more likely to escalate in physical fights when the opponents are well matched with respect to size, familiarity, and prior experience than when they are not (Maynard Smith, 1982; Stamps and Krishnan, 1994a).

The first encounters within dyads of conspecific *P. sicula* and *P. melisellensis* are consistent with future social interactions among individuals. Indeed, the direction and magnitude of the interactions exhibited during the first encounter per dyad parallel differences in thermal microhabitat use during prolonged encounters for that dyad. Dyads in which one lizard was clearly more aggressive than its opponent during their first encounter subsequently showed the largest difference in thermal microhabitat use, and it was the most aggressive individual that spent more time in the most thermally favorable portions of the terrarium. In pairs that exhibited low contrasts of aggression indices and basking time during the first encounters, between-individual differences in thermal microhabitat usage during the prolonged trials were also relatively low. In these dyads, both lizards were often simultaneously active, jointly used the basking site, and seemed highly tolerant to each other. Thus, the intensity of the interactions between two individuals recorded during the first encounter remained approximately constant throughout the ensuing three weeks. This result contrasts that of a study in juvenile *Anolis* lizards (Stamps and Krishnan, 1994b), which rarely engaged in social interactions after an initial overt fight but interacted frequently after a less aggressive first interaction.

Theory assumes or predicts relationships between social behavior on the one hand and life-history parameters such as growth on the other. For example, the large family of models on optimal territory size is based on a common assumption: within a given patch of microhabitat, certain territory sizes should result in higher rates of energy accumulation or greater mating success for their owners (reviewed in Stamps and Eason, 1989). In our study, cohabitation of two conspecific lizards during prolonged encounters resulted in an increased divergence of their growth rates. Importantly,

this variation was not a continuation of divergences that existed when lizards were housed alone and therefore cannot be attributed to innate individual differences in growth rate. Furthermore, during the prolonged encounters differences in growth rate between paired individuals mirrored differences in thermal microhabitat usage, which in turn mostly reflect differences in duration of activity.

The body temperatures achieved by ectotherms during activity will affect the rate of biochemical and physiological processes and alter ecologically relevant performance capacities (Huey, 1982; Van Damme et al., 1991). The prolongation of the activity period and the achievement of precedence in access to a basking site may therefore have important consequences on capacities to capture and process food, and thereby on growth rates. Thus, the observed differences in growth rates can be interpreted as a direct consequence of variation in differential thermal microhabitat use within dyads. However, other mechanisms could be the cause of a reduced growth rate in competing lizards. For instance, social interference may trigger stress hormones that orchestrate physiological changes such as the mobilization of stored fat reserves (see Sinervo and Licht, 1991; Wingfield et al., 1998, and references within). The release of hormones during stressing conditions may also induce behavioral changes such as interruptions to feeding (Assenmacher, 1973; Axelrod and Reisine, 1984).

Regardless of the mechanism, variation in early growth rate might be important in determining subsequent life-history patterns of individuals comprising dyads. Small hatchling lizards can experience reduced survivorship and be more vulnerable to gape-limited predators than larger conspecifics (reviewed in Downes, 2001). In species with indeterminate growth, a large body size at a given age can favor mate acquisition (Díaz, 1993; Martín and Forsman, 1999) and increased breeding frequency and clutch size (Bauwens, 1999; Downes, 2001). Therefore, lizards that are subordinate and thus suffer reduced body size may have relatively low probabilities of escaping from predators and a compromised future breeding success.

An intriguing result from our study is that the outcome of first encounters and subsequent divergence in thermal microhabitat use and growth within that dyad paralleled differences between two lizards in thermal microhabitat use recorded when they were housed in isolation. An analogous situation has been demonstrated in several fish systems (Metcalfe et al., 1992; Titus and Mosegaard, 1991, and references within). For instance, in Atlantic salmon (*Salmo salar*), social status is reflected in otolith size in young fry and can be used as a predictor of future growth potential; fish with initially larger otoliths, which are also dominant, grow faster than fish with smaller otoliths (Metcalfe et al., 1992). Both otolith growth in fishes and thermoregulation in lizards are closely linked to metabolic rate (Avery, 1984; Huey, 1982; Metcalfe et al., 1992). Animals with higher metabolic rates would be active for longer periods and might also have an advantage in aggressive encounters, so they would tend to be dominant. This in turn would lead to their having faster growth rates, because more dominant individuals can obtain a disproportionate share of limiting resources such as food and basking opportunities.

Irrespective of the mechanism, the observation that differences between two lizards in thermal microhabitat use, when housed in isolation, predicted the outcome and consequences of both first and prolonged social encounters seems to weaken the interpretation that the outcomes of first encounters alone influence the ensuing social relations within a dyad. Rather, we hypothesize that subtle phenotypic differences between individuals determine social status during both first

and subsequent encounters. In other words, morphological and behavioral characteristics may determine the potential dominance of an individual, which will then win most of the interactions, including the first encounter. Previous studies on lizards and other animals have identified body size and prior social experience as traits that largely determine the outcome of initial social interactions and subsequent social hierarchies (Maynard Smith, 1982; Stamps and Krishnan, 1994a). The design of our experiments deliberately minimized the potential contribution of these traits, because we matched lizards for body size and used socially naive animals. As a corollary, we could single out individual variation in thermal microhabitat use, which in turn is largely determined by activity levels as a factor that influences the outcome of social interactions.

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