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ORIGINAL ARTICLE

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Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*)

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Abstract Ontogenetic habitat shifts have been documented in numerous fish and amphibians and in some reptiles. Intraspecific competition together with differential predation, prey size, social interactions, size-related thermal requirements, and morphological constraints on movement are often implicated in this ontogenetic habitat separation. In the current study, we combined field observation with experiments in seminatural arenas to test various hypotheses regarding the ontogenetic habitat shift that we have documented in the common chameleon. Juveniles (mean, 1 g) occupied low grasses and the adults (mean, 35 g) were found on bushes and trees. Overlap in habitat use between these two age classes was minimal. Our field experiments showed that juveniles actively avoid the presence of adults by concealment or flight. Adults readily attacked and consumed juveniles, regardless of their own mass. These results suggest that the risk of cannibalism towards juveniles is an important selective force behind the ontogenetic habitat shift observed in the common chameleon and may be important in other species too.

Keywords Cannibalism · Ontogenetic habitat shift · Common chameleon

Introduction

Ontogenetic habitat shift is a well-documented phenomenon. In vertebrates, it is most commonly observed in amphibians and fish (Polis and Myers 1985). In amphibia, the ontogenetic shift is due to the metamorphosis of aquatic tadpoles to terrestrial adults, a transformation that involves drastic morphological modifications (Holomuzki 1986). However, in fish and reptiles, ontogenetic habitat shift is often merely accompanied by changes in the diet (Andrews 1971; Scott et al. 1976; Bohlin 1977; Moermond 1979; Stamps 1983a; Lind and Welsh 1994). Ontogenetic habitat shift is frequently considered a result of competition between adults and juveniles. Interspecific competition between phylogenetically related species may lead to spatial or temporal niche separation (Schoener 1974; Stamps 1983b). Intraspecific competition may even have a greater impact as a result of the similarities between individuals. However, additional selection forces may lead to niche separation—differential predation, prey size, social interactions, size-related thermal requirements and morphological constraints on movement (Scott et al. 1976).

Much of the current knowledge on ontogenetic habitat shift in reptiles has been collected from the arboreal lizards of the genus *Anolis*. A correlation between body mass and branch diameter has been suggested as a key mechanism for reducing size-related intraspecific competition (Schoener 1970; Moermond 1979). Branch selection is influenced by the visual field from the perch and by movement competence of the different size groups (Scott et al. 1976; Irschick and Losos 1999). An ontogenetic habitat shift allows juveniles to avoid adults and minimize interaction with them (Irschick et al. 2000, 2005). Stamps (1983a) identified seven alternative hypotheses that could account for ontogenetic habitat shift in lizards:

(1) Food availability—prey consumed by adults is scarce in the habitat occupied by juveniles, and vice versa. Under such conditions, adults will be attracted to one habitat and juveniles to another, and diet overlap would be minimal.
(2) Perch sites—suitable perch sites for juveniles are common in one habitat but scarce in the other. Juveniles will be attracted to the habitat where suitable perches are abundant.

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(3) Thermal requirements—juveniles may have different thermal requirements and thus select habitats with appropriate basking sites.
(4) Morphological constraints—juvenile lizards are restricted to low herbaceous vegetation due to size-related morphological constraints on locomotion performance.
(5) Predator avoidance—juveniles select predator-free habitats or habitats that provide safe shelters.
(6) Interspecific aggression—competition from a different species excludes juveniles into a separate habitat.
(7) Intraspecific aggression—adults are aggressive towards juveniles. Ontogenetic habitat shift is a mechanism to minimize interactions with adults.

In many species, adults are aggressive towards juveniles and hatchlings. The most extreme act of intraspecific aggression is that of killing a conspecific. If the killed individual is eaten by a conspecific aggressor, it is considered an act of cannibalism, which is a special case of predatory interaction (Elgar and Crespi 1992). Filial cannibalism in teleost fish is a mechanism to adjust parental investment according to resources availability (Manica, 2002). However, cannibalism of adults on unrelated young can be viewed as a predatory act, where the young are fair game. Foster et al. (1988) imply that the cannibalistic tendency of adults is counteracted by the avoidance behavior of juveniles. The risk of being cannibalized may drive juveniles to adult-free habitats (Werner et al. 1983). Thus, ontogenetic habitat shifts may result from interactions between foraging needs and predator avoidance strategies (Stamps 1983a).

Traditionally, the impact of predation has been associated with the removal of prey. Recently, the importance of the risk of predation per se has been recognized as a modifier of the behavior of prey animals, and both the removal of prey and behavioral effects may operate (Lima 1998; Brown et al. 2001; Nelson et al. 2004). Nevertheless, the impact of cannibalism has been mainly considered through the removal of individuals only. As such, cannibalism is recognized as a potentially important regulator of populations. In crabs, insects, and fish, size-structured cannibalism can result in skewed age distributions and fluctuations in recruitment (Persson 1988; Orr et al. 1990; Smith and Reay 1991; Botsford and Hobbs 1995; De Block and Stoks 2004). In some species, cannibalism appears to have a stabilizing effect on population dynamics, resulting in stable recruitment (Hopper et al. 1996; Benoit et al. 1998). Yet, the behavioral effects of the risk of cannibalism have been only rarely considered (see Foster et al. 1988, for an exception).

In this report we provide evidence for an ontogenetic habitat shift and for cannibalism in *Chamaeleo chamaeleon*. We evaluate the support for each of the hypotheses outlined above using our observational and experimental data. We conducted three sets of experiments. The first set evaluated the habitat selection of juveniles when adults are not in the vicinity. The second set tested the effect of adult presence on foraging mode of juveniles, and the final set tested whether juveniles are at risk of predation by adults.

Materials and methods

Study animals

The common chameleon, *C. chamaeleon*, is an arboreal species that occupies natural forests and plantations in the Mediterranean zone (Hódar et al. 2000). Chameleons are slow-moving diurnal lizards, highly adapted to arboreal life (Bickel and Losos 2002). Their strong digits, as well as their prehensile tail, have evolved to tightly grip the branches. They rely mostly on their adjustable camouflage to approach prey and avoid predation, but coloration depends on other factors, too, apart from the background color, such as temperature, social interactions, and breeding state (Cuadrado et al. 2001). In Israel, chameleons are active mostly during the warm months (May–November). Copulations occur in July–September. During October–November females deposit 14–47 eggs, which remain underground for 10 months of incubation (Keren 2001).

Study site and data collection

The study was conducted along a 14-km strip of the Mediterranean coast, in the foothills of Mt. Carmel, Israel. Observations and field manipulations were carried out at the entrance to Nahal Me'arot Nature Reserve (32°40′E, 34°57′E). The study site is a relatively dry habitat covered by a Mediterranean park forest. The trees (*Ceratonia siliqua*, *Pistacia lentiscus*, *Quercus calliprinos*) are short (2–5 m) and sparse, making it easy to walk through. Gaps between trees are extensive and are covered by perennial shrubs and annuals, which are dry during the summer months. The climate is characterized by moderate temperature means and moderate fluctuations. In summer, maximum and minimum daily temperatures are 30 and 21°C, respectively, and relative humidity averages about 70%. Mean annual rainfall is 550 mm, and it falls only during winter months (November–March).

Fieldwork was undertaken in May–October 1999, August–October 2000, and August–September 2004. Juveniles were defined as individuals with mass range of 0.6–1.9 g (age ranged from a few days to a few months). Adults were considered as any individual that weighed more than 13.3 g (1 year of age or older). Chameleons were collected from vegetation with the aid of a spotlight during the night, when their body is light in color and reflective. Each animal was individually marked by a series of tiny (scale size) colored dots of acrylic dye, weighed, and measured [snout–vent length (SVL), tail length (TL), and front leg diameter]. We used a water-based acrylic dye that was visible on the animals for only few weeks, and marked animals showed no ill effects. For each capture, we also recorded height off the ground, azimuth from the center of the shrub, branch diameter, and overall height and diameter of the shrub. Processed chameleons were returned at night to the exact location in which they had been captured.

Behavioral observations were conducted on each animal on the morning following its capture. We recorded the

number of movements per minute and proportion of time spent moving. Adults and juveniles were monitored for a minimum of 70 and 23 min, respectively. These time frames were determined as the point of asymptote in individual plots of moves per minute as a function of the observation period, calculated for 15 juveniles and 19 adults. Five additional variables were recorded during observations. (1) Foraging height—prior to the observation session, we set a 3.5-m metal pole adjacent to the capture location in a shady spot. A measuring tape aligned along the pole allowed height estimation for the focal animal. (2) Branch diameter—with the aid of binoculars we estimated branch diameter by comparing the known leg diameter to the branch on which the chameleon was holding. (3) Horizontal position—the horizontal surface between the central axis (e.g., tree trunk) and the outer most branches was divided into two equal radii circular planes. Based on relative position, we assign the animal to the inner or outer circle. (4) Azimuth—we measured the azimuths of the animal in relation to the direction of the sun. (5) Air temperature—we attached four thermocouples at increasing height (25, 50, 100, and 200 cm) along the pole. During observations, we recorded air temperature for all heights at 30-min intervals.

Diet analysis

Data on diet were collected using two approaches. (1) We collected scats from captured individuals used in the experiments (see details below) and stomach contents from road kills. Scats and stomach contents were sieved and categorized into ordinal level under a dissecting microscope, and frequencies of occurrence were calculated. (2) Direct observations of individuals capturing prey in the wild were carried out with the aid of binoculars.

Experiments

Experiment 1 In this experiment, 15 adults and 15 juveniles were individually tested to evaluate habitat preference and foraging mode when conspecifics are absent. We constructed in the field two temporary enclosures (3 m in diameter) made of 60-cm-wide polypropylene sheets. The sheets were inserted 10 cm below ground surface to prevent the escape of enclosed animals and the penetration of individuals from the outside. The location of each enclosure was chosen to include a tree, a bush, and perennial grass cover. In each experiment only one individual (adult or juvenile) was placed in each enclosure for 1–12 h. We recorded the microhabitat selected by the chameleon, height off the ground, branch diameter, horizontal position, and azimuth. These data were collected at 30- to 60-min intervals from a 5-m distance using binoculars.

Experiment 2 We examined the foraging behavior of juveniles in the presence of an adult. For the control, we tested the foraging behavior of juveniles in the presence of another juvenile. Two 1.5-m-long branches were placed vertically 1 m apart using metal stands, and set on a north–south axis. In each session, an adult was placed on a northbound branch and a juvenile on the opposite branch such that both individuals were on the same plane and on the same level from the ground. We divided this imaginary plane into eight equal segments, centered around the tree axis, and during observations recorded the spatial position of juveniles accordingly. Experiments were conducted on 30 juveniles, and these were presented either with an adult or a juvenile. At each session the focal juvenile was constantly observed for 25 min, and its position in relation to the other individual and the sun recorded. We also recorded number of movements per minute and the proportion of time spent moving. All sessions were carried out during morning hours.

Experiment 3 To test whether juveniles constitute potential prey for adults, we presented either a juvenile chameleon or a cricket (of the same size) to adults (n=20; mass range 15–56 g). Because the results from experiment 2 indicated that juveniles modified their behavior in presence of adults, we wanted to ascertain that the presented juveniles are not aware of the presence of the adults. A one-way reflective glass plate (40×60 cm) separated between adults and prey such that juveniles were not able to see the adults, but adults could view the prey offered. Adults were collected on the night before experimentation. Each animal was kept overnight (about 8 h) housed separately in a small plastic terrarium (25×15×15 cm) at room temperature (about 20°C). The next morning, we placed each one in the experimental arena, on a branch situated about 10 cm from the glass. On the opaque side of the glass, we placed a pot with dry grass, similar to the grass often used by juveniles in the field. At each session, a single chameleon juvenile or a cricket was placed on the grass, 10 cm away from the glass. Each adult individual was used for a single experiment only. At each session, we observed the adult for up to 30 min, but the experiment was terminated if the adult projected its tongue towards the prey or if the prey moved out of the experimental arena. We were able to prevent actual consumption of the juvenile chameleons in this experiment thanks to the separating glass, yet the projection of the tongue indicated that the adult attacked the prey offered, and thus poses a risk to it. The chameleons were released back at their collection site immediately upon completion of the experiments.

Results

In this study, we captured and collected data from 54 adults and 67 juveniles. Mean adult mass was 34.7±15.2 g (SD), with females being heavier than males (t_{51}=9.7, P<0.001; 36.7±15.1 and 27.1±10.3 g, respectively). However, there was no significant difference between the sexes in SVL (t_{51}=1.8, P=0.11; 10.5±1.8 and 9.8±2.1 cm for female and male, respectively) or TL (t_{51}=1.0, P=0.24; 10.8±1.8 and

11.1±1.9 cm, respectively). Juveniles were, on average, 34 times lighter than adults (t_{118}=62.4, P<0.001; 1.0±0.3 and 34.7±15.2 g, respectively), and about three times shorter in SVL (t_{118}=30.8, P<0.001; 3.7±0.4 and 10.1±2.0 cm for juveniles and adults, respectively) and in TL (t_{118}=37.8, P<0.001; 3.6±0.3 and 11.0±1.8 cm for juveniles and adults, respectively).

Juveniles foraged at significantly lower positions than adults. This pattern was observed both in free-ranging foraging individuals (t_{35}=8.7, P<0.001) and during experiment 1, in the enclosures (t_{28}=6.5, P<0.001; Fig. 1). Free-ranging adults foraged at an average height of 200.9 cm and juveniles at 57.3 cm. The vertical position of an individual correlated with vegetation height. Adults placed themselves nearly at the top of the vegetation [slope=1.02, r^2=0.70, $F_{(1,20)}$=44.4, P<0.001], whereas juveniles climbed to about four fifths of vegetation height [slope=0.85, r^2=0.40, $F_{(1,15)}$=9.4, P=0.008]. We did not detect any dependence between body mass and foraging height in juveniles [$F_{(1,15)}$=0.5, P=0.47] or in adults [$F_{(1,20)}$=1.0, P=0.31].

We recorded air temperature at four heights (25, 50, 100, and 200 cm) between 0600 and 1900 hours on 19 days during July–August 1999. Mean air temperatures were similar at all heights except between 1200 and 1500 hours, when mean temperatures at 50 cm and below reached 36°C, while above 100 cm temperatures were about 31°C. To remove the effect of ground heat radiation during midday, we conducted our observations and experiments during the morning hours, when air temperature did not differ between heights [$F_{(3,196)}$=0.64, P=0.59]. Furthermore, we examined the effect of temperature on foraging height by correlating the two variables for two time frames (0800–0929 and 0930–1100 hours). Records for each individual were averaged across each time frame to eliminate pseudoreplication. Foraging height was independent of temperature for both time frames (r=−0.17, n=19, Z=0.72, P=0.47 and r=0.17, n=24, Z=0.77, P=0.44, respectively).

Adults foraged on thicker branches than juveniles both in nature (t_{35}=2.1, P=0.041; Fig. 2) and in the enclosures (t_{28}=3.7, P<0.001). Branch diameter was associated with foraging height [r=0.50, $F_{(1,35)}$=11.5, P=0.002], but this association disappeared after controlling for plant size [residuals, r=0.21, $F_{(1,34)}$=1.6, P=0.22]. Branch diameter was not associated with body mass within age classes (r=0.14, n=21, Z=0.60, P=0.55 and r=0.02, n=16, Z=0.05, P=0.95 for adults and juveniles, respectively).

To estimate individual position, we divided the horizontal plane of the plant into an outer circle and an inner circle, whose radius was half the radius of the whole plant. Because the area of the outer circle was three times greater [$\pi(2r)^2-\pi r^2$, where r is the radius of the inner circle] than that of the inner circle (πr^2), the probability that an individual moving at random would be found in the outer circle was three times higher than for the inner circle. We used the ratio of 1:3 to calculate the expected number of individuals in the inner and outer parts, and compared these with the observed locations using a chi-square test. Both adults (χ^2_1=56.3, P<0.001 and χ^2_1=15.7, P<0.001 for free-ranging foragers and for individuals in the enclosures, respectively) and juveniles (χ^2_1=40.6, P<0.001 and χ^2_1=13.7, P<0.001 for free-ranging juveniles and for those in the enclosures, respectively) preferred the inner circle (nearby the center of the plant).

Direct observations on individuals and the position of an individual relative to the azimuth of the sun at time of observation were used to determine if it was primarily in a sunny or shady location. Free-ranging adults were observed more frequently than expected in a direct sunlight quarter: 0–90° (χ^2_3=11.8, P<0.05) but showed no significant preference between shade and direct sunlight (χ^2_1=0.6, P=0.45). In contrast, free-ranging juveniles were observed more frequently than expected in shady quarters: 180–270°, 270–360° (χ^2_3=47.4, P<0.01), and showed a preference for shady spots (χ^2_1=4.3, P=0.04). Adults and juveniles in the enclosures showed no significant preference between the

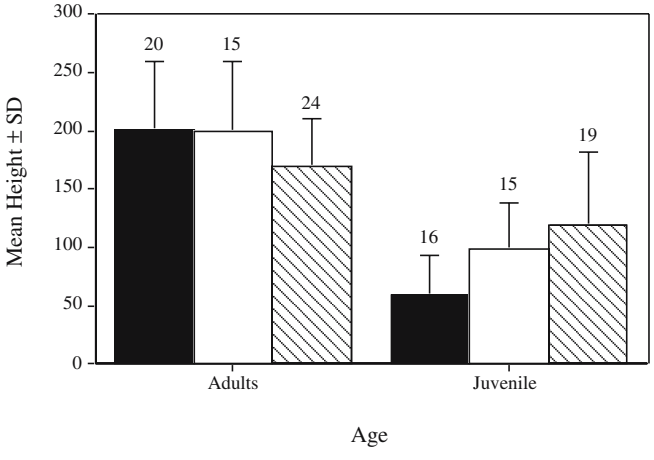


Fig. 1 Mean height (±SD; cm) for adult and juvenile chameleons foraging in nature (*black bars*), in enclosures (*white bars*), and at sleeping sites (*streaked bars*). *Values above bars* are sample size

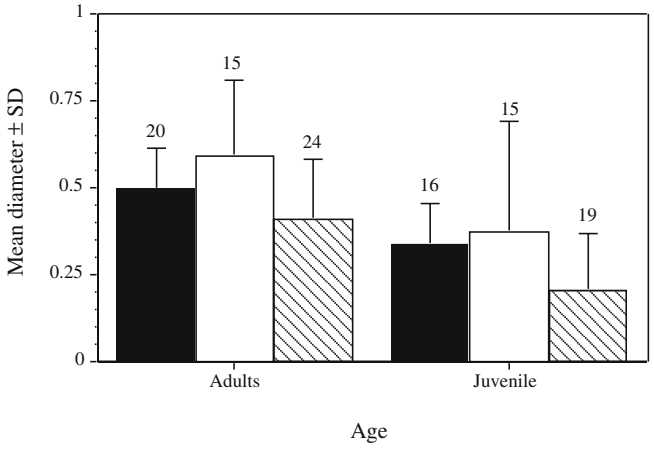


Fig. 2 Mean branch diameter (±SD; cm) for adult and juvenile chameleons foraging in nature (*black bars*), in enclosures (*white bars*), and at sleeping sites (*streaked bars*). *Values above bars* are sample size

quarters (χ^3_2=1.7, P=0.62 and χ^3_2=0.3, P=0.96, respectively) and between shade and direct sunlight (χ^2_1=0.2, P=0.68 and χ^2_1=3.5, P=0.06, respectively).

Sleeping adults were found at higher places (170.0± 40.7 cm) than juveniles (119.1±62.2; t_{41}=3.2, P<0.005; Fig. 1). Sleeping sites were associated with plant height [slope=0.45, r^2=0.32, $F_{(1,23)}$=10.4, P=0.004 and slope= 0.46, r^2=0.50, $F_{(1,14)}$=12.8, P=0.003 for adults and juveniles, respectively], and showed that chameleons preferred to sleep at midheight of plants. Adults spent the night on thicker branches than juveniles (t_{41}=3.9, P<0.01). None of the adults were found asleep on grass, whereas 91.5% of juveniles spent the night on grass (Fisher's exact test; χ^2_1=52.3, P<0.001).

The results of experiment 2 indicated that juveniles avoid adults. The direction of movement of juveniles in the presence of an adult was significantly different compared with the situation when another juvenile is present nearby (t_{28}=6.73, P<0.001). In all cases, juveniles moved away from the adult's location to the opposite side of the plane and behind the grass (one group t test: t_{14}=20.0, P<0.001). In contrast, juveniles in the experiment moved around at random in the presence of another juvenile (one group t test: t_{14}=0.53, P=0.60).

The foraging mode of adults was more sedentary than that of juveniles [$F_{(3,62)}$=14.6, P<0.0001 and $F_{(3,62)}$=30.0, P<0.0001 for proportion of time moving and mean moves/ min, respectively; Fig. 3]. Both the proportion of time spent moving (Scheffe's post-hoc test; P<0.001) and the rate of movement (P<0.001) were higher in juveniles. Nonetheless, juveniles in the presence of an adult reduced their proportion of time spent moving (P<0.001) and rate of movement (P<0.001) relative to solitary juveniles. The presence of another juvenile also diminished activity relative to solitary juveniles (P=0.001 and P=0.002 for proportion of time spent moving and rate of movement, respectively). Juveniles froze for 10–20 min in 47.4% of the times (n=19) when an adult was present nearby, and in 66.7% of the times (n=15) when another juvenile was introduced. However, 31.6% (n=15) of juveniles dropped to the ground and fled when they encountered the adults, but only one (6.7%) did so in the presence of another juvenile. Finally, during one of our field experiments an adult individual captured and rapidly consumed the juvenile on the neighboring branch.

In experiment 3, 60% of adults (n=10) projected their tongue at the cricket, and 30% of adults (n=10) tried to consume a juvenile. In this experiment, attack rate of juveniles did not differ from that of crickets (comparison of two proportions: Z=1.342, P=0.18; Zar 1984). Juvenile attack was independent of adult size (logistic regression, r^2=0.01; log-likelihood=6.1). In other words, the act of cannibalism of juveniles is not exclusive to the largest adults.

We collected scats from 51 individuals (22 adults and 29 juveniles), and stomach content from ten adults that were found dead (roadkills). Overall, diet composition of juveniles differed significantly from that of adults (chi-square test by permutations for scats data; χ^2_7=183.1,

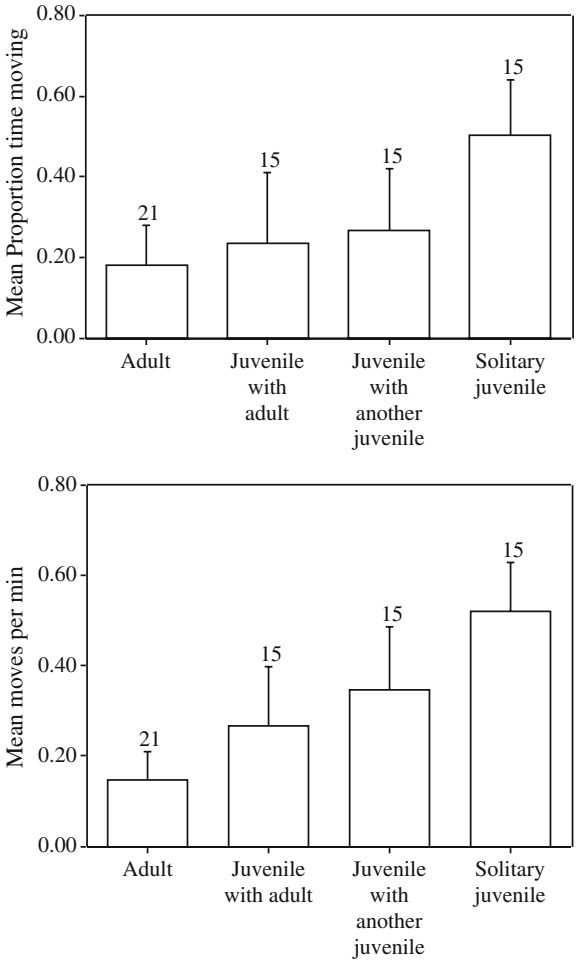


Fig. 3 Proportional time spent moving (±SD; *top*) and mean moves per minute (±SD; *bottom*) of adults, juveniles in the presence of an adult, juveniles in the presence of another juvenile, and solitary juveniles. *Values above bars* are sample size

Table 1 Diet composition of adult and juvenile chameleons based on scats and stomach contents

Food item[a]	Adults (stomach)	Adults (feces)	Juveniles (feces)
Hymenoptera	6 (22.2)	147 (57.4)	123 (36.2)
Coleoptra	3 (11.1)	25 (9.8)	45 (13.2)
Diptera	2 (7.4)	9 (3.5)	53 (15.6)
Hemiptera	3 (11.1)	8 (3.1)	35 (10.3)
Orthoptera	4 (14.8)	4 (1.6)	2 (0.6)
Aranea	0 (0.0)	2 (0.8)	51 (15.0)
Mantodea	0 (0.0)	1 (0.4)	0 (0.0)
Mollusca	0 (0.0)	1 (0.4)	0 (0.0)
Odonata	1 (3.7)	0 (0.0)	0 (0.0)
Homoptera	0 (0.0)	0 (0.0)	30 (8.8)
Lepidoptera	0 (0.0)	0 (0.0)	1 (0.3)
Fruit	8 (29.6)	59 (23.0)	0 (0.0)
Total	27	256	340

[a]Values are frequency and percentage (in parenthesis) of food items in the diet

$P<0.001$; food categories with low frequencies were combined). The most common food item in the scats for both juveniles (36%) and adults (57%) were Hymenoptera (Table 1). Beetles (Coleoptera), flies (Diptera), and bugs (Hemiptera) were also frequent in both age groups. However, spiders (Aranea) and cicadas (Homoptera) were consumed mostly by juveniles, whereas only adults consumed fruits (Table 1). Sixteen (73%) scats collected from adults contained invertebrates and fruits, and six (27%) had invertebrates only. Stomach content of adults shows similar composition as in scats but frequencies are too few for statistical testing. In addition to the difference in composition, juveniles consumed much smaller prey than adults. Finally, only on three occasions were we able to identify the prey via direct observation during consumption. On these occasions, the prey were a grasshopper, a small fruit, and a juvenile chameleon.

Discussion

Our data provide unequivocal evidence for ontogenetic habitat shift in the common chameleon. Juveniles are found on low vegetation, whereas adults occupy trees and large bushes. These two age categories do not spatially overlap. Such complete lack of overlap between age categories is common in amphibians and fish (e.g., Bohlin 1977). There are numerous examples of fish species in which the young are clustered into groups that occupy shallow water or the cover of rocks and submerged roots at the water edge, and do not venture into the deeper, open water. These water-edge habitats often lack the presence of adults. In *Anolis aeneus*, the adults remain in shady areas and the juveniles occupy the sunny clearings (Stamps 1983a). The *Anolis* group also shows habitat shift based on branch diameter; smaller individuals select thinner branches (Scott et al. 1976), and use lower perches (Irschick et al. 2000). However, in contrast to our system, the *Anolis* segregation is not strict, because all age classes can temporarily occupy the same plant.

Adult chameleons were also found on high parts of trees in Spain. Hódar et al. (2000) pointed out that the lower parts of trees (<1 m) were not used for feeding and basking, only during movements between plants. The fact that we measured high temperatures at a height of 0.5 m between 1200 and 1500 hours emphasizes the question: What are the factors that cause the juveniles in our study to occupy exclusively a habitat that differs from that of adults, that reaches extremely high temperatures, provides less shade, and offers smaller protection from predators?

Below, we evaluate the support for each of the hypotheses formerly put forward (Stamps 1983a) as possible causes for the ontogenetic habitat shift in the common chameleon.

Food availability In some reptiles, juveniles have a different diet than adults (e.g., water snakes, Mushinsky et al. 1982; slider turtles, McCauley and Bjorndal 1999). Diet differences may imply that juveniles have to forage in habitats rich with their specific food, which may be separate from the feeding sites of adults. Lind and Welsh (1994) showed age-related dietary shifts in water and sea snakes. Dietary shift as a function of size is expected in most carnivorous reptiles, because as individuals increase in size they can consume larger prey. Overall, both chameleon age classes consumed mostly invertebrates (100% of food items in juveniles and 77% in adults; Table 1). Nevertheless, the fact that juveniles and adults differed in both indices of foraging mode (with juveniles foraging more actively) suggests that their diet may differ (Huey and Pianka 1981). In our study site, invertebrates were common in both low and high vegetation. Edible fruits were most often found on trees and bushes, but also on semishrubs such as *Osyris alba*, and on perennial herbs and vines such as *Rubia tenuifilia* and *Smilax aspera*. Furthermore, fruits of short trees and bushes often grow a few centimeters above the ground and are therefore available for juvenile chameleons, yet none was found in the juveniles' scats. Regardless of food availability differences that may exist between the habitats, Hymenoptera of all sizes were the most abundant prey for both adults and juveniles. That finding led us to conclude that dietary preference seems unlikely as the main cause for the habitat shift since the primary food item for both ages is similar.

Perch sites Selection of branch diameter as a function of individual mass has been demonstrated for *Anolis* (Scott et al. 1976). We found that juveniles forage on thinner branches than adults do. This result makes sense in terms of the grasping ability of the smaller toes of juveniles. Moreover, adults are unlikely to exploit thin branches because these cannot support their greater body mass. This result may also stem from a possible independent preference of juveniles for lower and grass-like vegetation. By foraging on small and grass-like vegetation, thicker branches are not a valid selection for juveniles because they are not available on such plants. Nevertheless, on all the trees or bushes used by adults, we observed a wide range of branch diameter, from 1 mm at the plant edge to 1 cm or above near the center. All of the shrubs or trees used by adults had a wide selection of branch diameter, from the thickest used by adults to the thinnest used by juveniles. Chameleons, unlike any other lizard, have a zygodactyl foot in which adjacent digits are fused on each foot, forming opposing grasping pads. The combination of the grasping feet and a prehensile tail allows juveniles to move at the periphery of trees from one thin branch to another without traversing larger branches in between. Nonetheless, juveniles did not use thin branches on shrubs and trees. Hence, branch diameter is not a selective force for habitat segregation between juveniles and adults.

Thermal requirements Poikilothermic vertebrates may shift habitat following changes in ambient temperature. Although juvenile *Anolis* occupied clearings, they avoided direct sunlight, and stayed mostly at the edges of clearings (Stamps 1983a). Even though our habitat did not include a forest with sunny clearings, we found that juvenile cha-

meleons acted similarly to the *Anolis* and preferred shady spots. In contrast, adult chameleons showed no preference. Furthermore, we did not detect an association between temperature and foraging height. In fact, our observations imply the opposite from what is expected of poikilotherms. Juveniles weighing about 1 g should reach optimal body temperature much faster than an adult of 20–40 times their size. Exposure to direct sunlight would overheat a small body quicker than a large one. In addition, overheating is more serious as one approaches ground level because of heat radiation reflected from the ground. Temperature differences between the two habitats in the afternoon cannot account for the habitat choice of juveniles in the morning, a time when the two habitats provide similar temperatures. Moreover, if the hotter afternoon temperatures close to ground were a key factor in habitat selection of juvenile chameleons, we would expect juveniles to escape ground radiation by climbing up into trees and bushes. We cannot rule out the possibility that had the experiments been performed in the afternoon, the preference of the juveniles would have been more similar to that of the adults. Yet, this possibility only emphasizes that we need to seek other explanations for the habitat segregation observed in the morning.

Morphological constraints Moermond (1979) suggested that the performance of juvenile locomotion, relative to that of adults, is inferior. However, young Komodo dragons (*Varanus komodoensis*) are agile tree climbers, whereas full-grown adults are too heavy to climb and they keep to the ground (Murphy et al. 2002). Adult chameleons are able to climb trees efficiently. Juvenile chameleons foraged on average at about 50 cm off the ground under natural conditions. Yet, when placed on their own in an enclosure, they reach a maximum foraging height of 252 cm. Under the same conditions, the maximum sleeping height for juveniles was 240 cm. These maximal records demonstrate that juveniles have the ability to forage at adult height, but do not do so for reasons other than morphological impediment.

Predator avoidance Jackson (1961) and others have proposed that small size classes of fish are restricted to microhabitats providing cover until they outgrow their important predators. The basic assumption behind this idea is that the important predators do not occur or are not efficient in these microhabitats. Chameleons in Israel have numerous predators: several snake species (*Malpolon monospessulanus*, *Coluber ravergieri*, etc.), kingfishers (*Halcyon smyrnensis*), birds of prey (*Falco tinnunculus*, *Circaetus gallicus*, *Tyto alba*), rats (*Rattus rattus*, *R. norvegicus*), and small arboreal carnivores (e.g., *Martes foina*; Schleich et al. 1996; Keren 2001). Other small carnivores (e.g., *Vulpes vulpes*, *Herpestes ichneumon*, *Meles meles*) are potential predators for individuals that travel on or close to the ground. Out of this list of common predators, only the snakes, rats, and the stone marten are arboreal or hunt both on the ground and on trees. The kingfisher and the birds of prey usually pick their prey off the ground, and do not pursue them into dense vegetation. Chameleons cannot outgrow any of these predators, but because most of the latter are terrestrial, rather than arboreal, living as high as possible off the ground should reduce predation. However, our observations of juveniles show the opposite from the expected by the predator avoidance hypothesis: smaller individuals are mostly found in the habitat where more predators are present. There are very few predators that will be avoided by living on grass and close to the ground. One such predator that comes to mind, however, is the adult chameleon (see Intraspecific aggression).

Interspecific aggression In a series of experiments, Gerber and Echternacht (2000) showed that a larger congener may have a significant impact on a smaller target species by preying on small individuals. Intraguild predation provides benefits not only through energetic gain, but also eliminates potential competitors (Polis and Holt 1992). In an identical manner to predation pressure, intraguild predation can drive the small size class of the target species to shift into a habitat that lacks the congeneric predator. In Israel, *C. chamaeleon* is the only chameleon species in the Mediterranean habitats (Bouskila and Amitai 2001). Of the lizards in Israel that thrive on trees, only *Laudakia stellio* is large enough to pose a significant risk to juvenile chameleons: all other lizard species that could potentially prey on young chameleons are terrestrial or subterranean. Nevertheless, even *L. stellio* is not likely to be a significant predator for juvenile chameleons on trees, because it lacks the ability of chameleons for grasping thin branches, and it uses only the thickest branches and the trunks of trees.

Intraspecific aggression Schall (1974) and Bohlin (1977) have associated ontogenetic habitat shift in juvenile lizards and fish with competitive exclusion between different age classes. As with some other reptiles, adult chameleons may pose a real risk of predation on juveniles (Polis and Myers 1985). We found that when juvenile chameleons were faced with an adult they manifested drastic changes in behavior, moved away, and reduced their activity. Several individuals froze continuously for 10–20 min; others dropped to the ground and rapidly moved away. These behaviors are typical in the predator avoidance repertoire of chameleons (Cuadrado et al. 2001). Colley et al. (1989), who documented cannibalism in salamanders, showed that juvenile salamanders avoided the presence of adults by actively shifting between habitats. Our observation of an adult consuming a juvenile, and the fact that adults attacked juveniles in a similar way to attacks on other prey in experiment 3, support the idea that cannibalism is an important driving force for the ontogenetic habitat shift in the chameleons. We did not detect chameleon remains in scats and stomach contents of adults, suggesting that cannibalism is a rare event under natural conditions (Colley et al. 1989). This is not surprising, because juveniles seldom overlap with adult habitat, and when they do overlap, they employ behavior to reduce the probability of being devoured by an adult. However, the

fact that adults readily consume juveniles when the opportunity arises suggests that such intraspecific aggression by adults can select for individuals that inhabit low herbaceous vegetation.

Why do juvenile chameleons not select the thin branches within a tree as a mechanism to avoid predation by adults? A comparison of the foraging mode indices of adults to those in the review by Perry (1999) reveals that chameleons are "sit-and-wait" predators. Although they are slow moving and rely on slow stalking tactics, they have two characters that make them highly efficient predators. First, chameleons have very sharp eyesight, thanks to a unique concave lens (Ott and Schaeffel, 1995). The eyeballs can rotate independently, and when both eyes are focused forward, the chameleon has complete binocular vision (Martin 1992). Such vision provides a mechanism to accurately estimate the distance to prey (Gans 1967; Ott et al. 1998). Second, although many lizard species use their tongue to capture small prey (Herrel et al. 2000), chameleons use a ballistic tongue projection mechanism that is unique among lizards. During prey capture, the tongue can be projected up to two full body lengths and may extend up to six times its resting length (Herrel et al. 2001). The ejected tongue reaches a speed of 5.8 m/s in 20 ms (Wainwright et al. 1991), and is supported by powerful retraction muscles and a suction mechanism at the mucus-covered tongue pad (Herrel et al. 2000, 2001). These morphological characters allow adult chameleons to reach prey at distances of 12–28 cm. In other words, adults could capture juveniles if these would use the thin branches on the trees, even if these branches were too thin to support adult weight, as long as the juveniles were no more than ≈20 cm from the adult position. Chameleons are able to handle larger and more aggressive prey than juvenile conspecifics (e.g., grasshoppers, praying mantis, and other lizards; Luiselli and Rugiero 1996; Pleguezuelos et al. 1999). Although perching on a tree would allow juveniles to escape many of the terrestrial and aerial predators, predation risk from adult chameleons is probably a stronger selective force than the combined selective pressure from other types of predation.

In this study, we documented an ontogenetic habitat shift in the common chameleon. We did not test experimentally all possible mechanisms suggested by Stamps (1983a,b), and thus they may still have some effect on the segregation between habitats of adults and juveniles. Nevertheless, based on our observational data, we found little support for most of the other suggested hypotheses, except the one that involves intraspecific aggression. We focused our experiments in this area, the intraspecific relations between adults and juveniles, and the results we obtained suggest it as an important cause for the observed habitat segregation. Because we could not evaluate the role of resource competition on top of the risk of aggression and predation in juveniles, our results do not necessarily point out in the direction of the importance of intraspecific competition (Connell 1975) nor imply a combination of competition and predation (e.g., Bouskila 1995). Additional experimental work is required, particularly on the impact of resource competition and food availability in the different habitats.

Our results suggest that intraspecific niche separation and the impact of adults on the foraging of juveniles result from potential aggression between size-class groups. The similarity between these findings and those in another lizard (*Acanthodactylus boskianus*; Hawlena et al. in press) and in the threespine stickleback (*Gasterosteus aculeatus*) (Foster et al. 1988) suggests that the link of aggression from adults towards juveniles (including cannibalism) with intraspecific habitat separation may be a more common phenomenon than previously realized. We suggest that even in cases where ontogenetic habitat shifts can be explained by intraspecific resource competition alone, the risk of aggression and cannibalism should be likewise considered and tested, because if they exist, they may add different aspects to habitat segregation between age groups.

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