The ontogeny of courtship behaviours in bat pups (*Saccopteryx bilineata*)

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Summary

In mammals, adult behaviour patterns are often expressed by juveniles throughout ontogeny. In bats, many social behaviours develop before pups are weaned, but the ontogeny of social behaviours in juvenile bats is largely unexplored. We studied bat pups' social behaviour, specifically the solicitations for maternal care in the greater sac-winged bat, *Saccopteryx bilineata*. Solicitation periods were prolonged (up to 25 min) and consisted of conspicuous behavioural interactions between pups and their mothers. Since solicitation periods could be initiated by pups or mothers, their duration is probably not caused by a conflict over nursing alone. Solicitation periods were the second most prevalent use of activity time in pups. Some pup behaviours resembled the courtship behaviours of adult males and these incipient courtship behaviours occurred most often within solicitation periods. Both length and complexity of solicitation periods increased significantly during ontogeny but there was no significant difference between male and female pups. Also, the activity outside of solicitation periods was not significantly different between pups of both sexes, even though their activity differs remarkably as adults. Prolonged solicitation periods of *S. bilineata* pups might be comparable to mammalian play and potentially function as practice for adult courtship behaviours.

Keywords: behavioural ontogeny, maternal care, motor-training hypothesis, play.

Introduction

The behavioural repertoire of a mature animal cannot be fully understood without knowledge of the ontogenetic origins of the animal's behaviour

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(Welker, 1971; Bekoff, 1972). The social environment can have extensive effects on the development of an animal's behaviour (White et al., 2002), and the first social unit in mammals consists of a mother and her offspring (Wilson, 1975). The mother–offspring bond and the resulting maternal investment have a prominent influence on the ontogeny of behaviour in various mammalian species including cetaceans (Gibson & Mann, 2008), ungulates (Pratt & Anderson, 1979) and primates (Suomi, 2005). Chiropterans exhibit post-natal maternal investment through nutritional support such as lactation (Kunz & Hood, 2000) and, in some species, food-provisioning (Vehrencamp et al., 1977; Wilkinson, 1984; Raghuram & Marimuthu, 2007). Nonnutritional maternal support includes allogrooming (McLean & Speakman, 1997), thermoregulation, transport and protection (Kunz & Hood, 2000). The acquisition of foraging techniques by pups can benefit from maternal investment as well (Brigham & Brigham, 1989). However, no evidence for maternal influences on pup social behaviours exists so far.

We studied the development of social behaviours in pups of the greater sac-winged bat, *Saccopteryx bilineata*. The mating system of *S. bilineata* can be described as resource defense polygyny because males try to monopolize groups of females by granting them access to a roosting territory in the day-roost that they defend (Emlen & Oring, 1977). Territorial and courtship displays of adult males are energetically costly activities that are used to defend harem boundaries and retain females (Voigt et al., 2008). The complex courtship displays of males consist of a number of olfactory cues, visual displays and vocalizations that have been documented thoroughly (Bradbury & Emmons, 1974; Bradbury & Vehrencamp, 1976; Voigt et al., 2008). The development of these behaviours has not been examined yet. Courting males typically approach one perched female at a time from above or the side by crawling horizontally in a fitful manner or by landing in close proximity (Tannenbaum, 1975; Behr & von Helversen, 2004; see supplementary video 1 at http://media.brill.nl/beh/147/5-6/). During the approach, the males utter courtship songs (Behr & von Helversen, 2004). Approaches are often preceded or followed by hover displays in front of females, which represent the most conspicuous component of adult male courtship behaviour (Tannenbaum, 1975; Bradbury & Vehrencamp, 1976; Voigt et al., 2006, 2008). During hovering, males often fan odor toward female conspecifics and simultaneously omit a stereotypic whistle (Voigt & von Helversen, 1999; Behr &

von Helversen, 2004). However, hovering may also occur without odor fanning and vocalizations (Voigt & von Helversen, 1999). Even though courting males frequently change their position in the roost by crawling or flying, the courted females remain stationary. When females are unresponsive to males' courtship displays, they generally do not evade the courting males, but rather fend them off aggressively (Tannenbaum, 1975).

Previous field observations have shown that *S. bilineata* pups exhibit a conspicuous solicitation period in order to receive maternal care (authors' personal observations). Solicitation periods involve visual and vocal displays by the pups and, to some degree, by the mothers. This behaviour is probably energetically costly and risky due to increased vulnerability to predation. Parturition is fairly synchronized within colonies and takes place from May to mid-June in Costa Rica (Bradbury & Vehrencamp, 1976). A female gives birth to one pup per year. Pups become volant at 2–3 weeks but may nurse for an additional 8 weeks (Tannenbaum, 1975). Females disperse at 2–3 months of age whereas male pups often stay in their natal colony (Nagy et al., 2007). In five seasons of working with *S. bilineata*, we never observed weaned pups behaving differently from adult conspecifics, which suggests that pups act as functional adults after weaning (authors' personal observation). Thus, relevant adult behaviours need to develop earlier in ontogeny. Many of the behaviours exhibited during adult male courtship (i.e., hovering and frequent position changes in the roost through crawling or flying; Tannenbaum, 1975; Behr & von Helversen, 2004) are occasionally also performed by pups.

We investigated whether the development of visual courtship behaviours are influenced by mother–pup interactions in *S. bilineata* using time-budget analysis with focal animal sampling (Altmann, 1974) in the day-roost. If solicitation periods function for practice of adult male courtship behaviours, we would expect an early ontogenetic expression of courtship behaviour to occur predominantly during mother–pup interactions, instead of occurring during the remainder of the pups' active time. In addition, we hypothesized that these incipient courtship behaviours are most pronounced in male pups.

Materials and methods

Research was carried out at La Selva Biological Station in Costa Rica (Organization for Tropical Studies; 10°25′N, 84°00′W) in the summers of 2005,

2006 and 2008. The study population was well habituated to humans, and the bats could be observed within a few meters at the daytime roost without causing noticeable disturbance. Roost sites are generally buttress cavities or the lower well-lit portions of trees, but colonies are also found on or in abandoned buildings (Bradbury & Vehrencamp, 1976). We differentiated individuals from one another with the aid of colour and number bands on their forearms (A.C. Hughes, size XCL). Non-volant pups were identified via their respective mothers; once volant, they were caught with mist nets (Ultrathin Mist Nets M-14, Ecotone, Sopot, Poland), sexed and banded.

Twenty-eight pups were studied using focal animal sampling (Altmann, 1974). We observed each individual on multiple sessions (range 8–10 sessions per pup) during ontogeny. In 2005 and 2006, 10 1-h observation sessions were conducted on each of 10 pups (4 females, 4 males, 2 unsexed) belonging to three different colonies. We also made additional observations on the behaviours of their mothers. Observation sessions in 2005 and 2006 began one week before the pups became volant (2–3 weeks of age) and continued until the pups were almost weaned (8–9 weeks of age). Observation sessions in 2008 started later (5–6 weeks of age) and continued until the female pups started dispersing from their natal colonies (10–12 weeks of age). In 2008, a minimum of eight 2-h observation sessions (range 16–20 h per pup) were recorded for each of 18 pups (7 females, 11 males) belonging to four different colonies. Pup behaviours were defined before focal observations began and behavioural categories were established (Table 1). Each behaviour type was considered either a state or an event (sensu Altmann, 1974). States had temporal durations (e.g., grooming), whereas events were instantaneous (e.g., yawning). Pups frequently uttered social calls during solicitation periods (Knörnschild et al., 2006; Knörnschild & von Helversen, 2008), but vocalizations were not quantified for this study. During observation sessions, the duration of states and the frequency of events were recorded for all 2-min periods of the session. The behavioural data were then averaged both within observation sessions and for every individual. We used parametric tests (two-tailed, $\alpha = 0.05$), except when sample sizes were $\leqslant 10$. In this case, the appropriate nonparametric tests were used, calculating exact instead of asymptotic p values (after Mundry & Fischer, 1998). Means $\pm$ SD are given unless stated otherwise. All statistical tests were conducted using SPSS version 11.5 (SPSS, Chicago, IL, USA). Bonferroni corrections were applied following Holm (1979).

Table 1. Ethogram describing behaviours exhibited by *Saccopteryx bilineata* pups.

Behaviour	Event/ state	Abbrevi- ation	Description	Behavioural category		
				1	2	3
Resting or resting on mother	State	R	Not moving; if attached to mother the pup may be nursing or resting on the teat			
Grooming	State	G	Tending to coat and wings, while hanging solo or attached to the mother by feet		X	
Resistance	State	RES	Refusing to let go of the teat when the mother wants the pup to detach			X
Solicitation	State	SOL	Soliciting maternal care though conspicuous visual and vocal displays	X		
Rocking	State	ROCK	Gentle rocking of body from side to side			X
Hover	Event	H	Hovering in air, no pronounced lateral or vertical movement	X		
Change position flying	Event	CPF	Flying from one position to another in roost site	X		
Change position crawling	Event	CPW	Crawling on wall to new position	X		
Prolonged flying	Event	F	Flying with no obvious destination, often returning to the same position	X		
Yawn	Event	Y	Both rows of teeth and gum exposed, mouth open		X	
Wing stretch	Event	WS	One wing fully stretched out		X	
Coating fur	Event	FUR	Stereotypic licking of wing and distribution of saliva on fur		X	
Push-up	Event	PU	Body moves off wall by pushing wrists against wall		X	
Wing aggression	Event	WA	Hitting conspecifics with folded wing			X
Dribbling	Event	D	Pounding wrists against wall, each movement is more defined than rocking			X
Change position on mother	Event	CPM	Changing orientation/position while attached to mother			X
Chewing	Event	CH	Obvious, stereotypic exposure of teeth while chewing saliva			X

Behaviours are assigned to categories by an "X" in the right columns: 1, movement behaviours (incipient courtship behaviours); 2, comfort behaviours; 3, miscellaneous behaviours.

In addition to field notes, a digital video camcorder (Canon ZR930) was used to record behaviours, and footage was viewed digitally through Windows Media Player v10. When possible, all pups of a specific study colony were observed simultaneously. Video footage aided in filling out the observational record for pups that were not in immediate view during the observation period. Although some observation sessions were partitioned to watch specific pups, the cumulative observation time for each pup in a session was equal.

Data collected in 2008 (18 pups) were used to describe pup solicitation periods quantitatively, whereas data taken in 2005 and 2006 (10 pups) were used to describe the initiation of solicitation periods and to compare solicitation periods at two ontogenetic phases (2–5 weeks and 6–9 weeks of age; each phase was represented by five observation sessions per pup; pups were already volant during both phases). We used both data sets to test for sex-specific behavioural differences.

Results

States and events

Pups spent the majority of observed time resting (82.1%) and the remaining time (17.9%) in active states consisting of grooming, resisting, soliciting, or rocking (Table 1). There was a significant difference between the percentages of time allotted to each state (repeated measures ANOVA with states as within-subject factor and both sex and colony as between-subject factor; test of within-subjects effects, lower-bound epsilon; state: $F_{1,13} = 64.033, p < 0.0001$, partial $\eta^2 = 0.831$; state $\times$ sex: $F_{1,13} = 0.196, p = 0.665$, partial $\eta^2 = 0.015$; state $\times$ colony: $F_{3,13} = 0.632, p = 0.608$, partial $\eta^2 = 0.127$), with grooming being the most frequent active behavioural state (69.5%), followed by soliciting (28.9%), resisting (1.2%) and rocking (0.4%). Differences between states were significant (multivariate test: $F_{3,11} = 73.785, p < 0.0001$, partial $\eta^2 = 0.953$; pair-wise comparisons: all $p \leqslant 0.005$) with the exception of resisting and rocking. Neither sex nor colony had a significant influence on the duration of states (test of between-subjects effects; sex: $F_{1,13} = 0.698, p = 0.419$, partial $\eta^2 = 0.051$; colony: $F_{3,13} = 0.521, p = 0.675$, partial $\eta^2 = 0.107$). We classified events into movement behaviours, comfort behaviours and a miscellaneous behaviour

category (Table 1). All of the movement behaviours displayed by pups were also part of the behavioural repertoire of courting adult males (see supplementary videos 1 and 2 for the similarity between pup behaviours during solicitation periods and adult male courtship behaviours; the behaviours displayed by both the pup and the adult male include hovering and changing position by crawling and flying). Hence, we termed these behaviours 'incipient courtship behaviours'. Movement behaviours included changing position by flying (CPF) or crawling on the wall (CPW), prolonged flying (F) and hovering (H). There was a significant difference between the occurrences of movement behaviours during observation periods (repeated measures ANOVA with movement behaviours (mov) as within-subject factor and both sex and colony as between-subject factor; test of within-subjects effects, lower-bound epsilon; mov: $F_{1,13} = 15.497$, $p = 0.002$, partial $\eta^2 = 0.544$; mov $\times$ sex: $F_{1,13} = 0.764$, $p = 0.398$, partial $\eta^2 = 0.056$; mov $\times$ colony: $F_{3,13} = 1.399$, $p = 0.288$, partial $\eta^2 = 0.244$; Figure 1). CPF and CPW occurred significantly more often than either F or H (multivariate test: $F_{3,11} = 11.758$, $p = 0.001$, partial $\eta^2 = 0.762$; pair-wise comparisons: all $p \leqslant 0.004$). Comfort behaviours included coating fur with saliva (FUR), push-ups (PU), wing stretches (WS) and yawns (Y). There was a significant difference between the occurrence of comfort behaviours (repeated measures ANOVA with comfort behaviours (com) as within-subject factor and both sex and colony as between-subject factor; test of within-subjects effects, lower-bound epsilon; com: $F_{1,13} = 47.983$, $p < 0.0001$, partial $\eta^2 = 0.787$; com $\times$ sex: $F_{1,13} = 1.355$, $p = 0.265$, partial $\eta^2 = 0.094$; com $\times$ colony: $F_{3,13} = 1.409$, $p = 0.285$, partial $\eta^2 = 0.245$; Figure 1), with WS occurring significantly more often than the other three events (multivariate test: $F_{3,11} = 15.486$, $p < 0.0001$, partial $\eta^2 = 0.809$; pair-wise comparisons: all $p \leqslant 0.005$, with the exception of PU and Y). The miscellaneous behaviour category consisted of chewing (CH), changing position while clinging to the mother (CPM), dribbling (D) and wing aggression (WA). There was no significant difference between the occurrence of these events (repeated measures ANOVA with miscellaneous behaviours (mis) as within-subject factor and both sex and colony as between-subject factor; test of within-subjects effects, lower-bound epsilon; mis: $F_{1,13} = 3.496$, $p = 0.084$, partial $\eta^2 = 0.212$; mis $\times$ sex: $F_{1,13} = 3.395$, $p = 0.088$, partial $\eta^2 = 0.207$; mis $\times$ colony: $F_{3,13} = 3.159$, $p = 0.061$, partial $\eta^2 = 0.422$). Neither sex
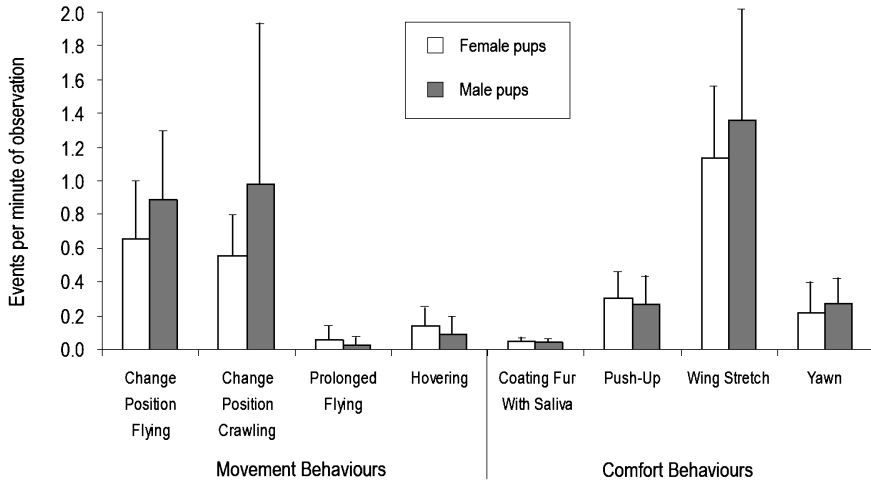
Figure 1. Occurrence of behavioural events displayed by juvenile *S. bilineata* that are incipient male courtship behaviours (movement behaviours) or comfort behaviours. Differences between males and females were not significant. For a detailed explanation of behaviours, see Table 1. Means ± SD are shown.

nor colony had a significant influence on the occurrence of movement behaviours (test of between-subjects effects; sex: $F_{1,13} = 1.255$, $p = 0.283$, partial $\eta^2 = 0.088$; colony: $F_{3,13} = 0.921$, $p = 0.458$, partial $\eta^2 = 0.175$), comfort behaviours (test of between-subjects effects; sex: $F_{1,13} = 1.208$, $p = 0.292$, partial $\eta^2 = 0.085$; colony: $F_{3,13} = 2.351$, $p = 0.120$, partial $\eta^2 = 0.352$) or miscellaneous behaviours (test of between-subjects effects; sex: $F_{1,13} = 0.019$, $p = 0.893$, partial $\eta^2 = 0.001$; colony: $F_{3,13} = 0.687$, $p = 0.576$, partial $\eta^2 = 0.137$). The presentation of odor, an important component of adult male courtship, was never observed in pups.

Initiation of solicitation periods

Solicitation periods were either initiated by the pup itself or by its mother. In the latter case, mothers hovered in front of pups, then flew away and perched in close proximity; this behaviour was repeated until the pup started soliciting. The initiation of solicitation periods by mothers was significantly more prevalent early in ontogeny than later (Wilcoxon signed rank test; $T = 1$, $N = 10$, exact $p = 0.004$; mean number of maternal hovers in front of pups per h: phase 1: 1.2 ± 0.3, phase 2: 0.8 ± 0.2).

Solicitation periods

Solicitation periods lasted more than seven minutes on average (7.82 ± 5.79 min, range $= 1$–26.5 min, $N = 102$; 18 pups). Solicitation periods did not always result in allowance of maternal care through nursing at their completion. When denied care, the pup either returned to resting or grooming. There was a significant difference between the length of successful solicitation periods in which the pup received maternal care and unsuccessful solicitation periods when care was denied (paired t-test; $t_{11} = 3.211$, $p = 0.008$; data on both successful and unsuccessful solicitation periods averaged per pup; we only observed both successful and unsuccessful solicitation periods for 12 pups). Successful solicitation periods (10.25 ± 6.86 min, range $= 1$–30 min, $N = 51$) were on average twice as long as unsuccessful solicitation periods (5.39 ± 4.17 min, range $= 1$–23 min, $N = 51$). Moving away from the pup without displaying aggressive behaviour was commonly found during prolonged solicitation periods and this evasive or inviting behaviour was clearly distinguished from maternal aggression towards the pup (i.e., hitting the pup with a folded wing or, rarely, biting the pup). Behaviours that occurred during solicitation periods included incipient courtship behaviours (movement behaviours) and, to a lesser degree, comfort behaviours (Figure 2). Incipient courtship behaviours were significantly more prevalent in solicitation periods than in other states (t-test for matched pairs, α adjusted according to sequential Bonferroni correction; CPF: $t_{17} = 7.685$, $p < 0.0001$, $\alpha = 0.0063$; CPW: $t_{17} = 2.789$, $p = 0.013$, $\alpha = 0.025$; F: $t_{17} = 2.364$, $p = 0.030$, $\alpha = 0.05$; H: $t_{17} = 4.319$, $p < 0.0001$, $\alpha = 0.0071$), whereas the opposite was found for comfort behaviours (t-test for matched pairs, α adjusted according to sequential Bonferroni correction; FUR: $t_{17} = -8.849$, $p < 0.0001$, $\alpha = 0.0083$; PU: $t_{17} = -5.170$, $p < 0.0001$, $\alpha = 0.01$; WS: $t_{17} = -4.952$, $p < 0.0001$, $\alpha = 0.0125$; Y: $t_{17} = -4.015$, $p = 0.001$, $\alpha = 0.0167$).

Ontogenetic changes

The percentage of time allotted to solicitation periods increased significantly during ontogeny (Wilcoxon signed rank test, α adjusted according to sequential Bonferroni correction; $T = 0$, $N = 10$, exact $p = 0.002$, $\alpha = 0.0125$; phase 1: $1.7 \pm 1.6\%$, phase 2: $9.7 \pm 4.8\%$), whereas the percentage of time spent resting decreased significantly (Wilcoxon signed rank test, α adjusted according to sequential Bonferroni correction; $T = 1$, $N = 10$, exact
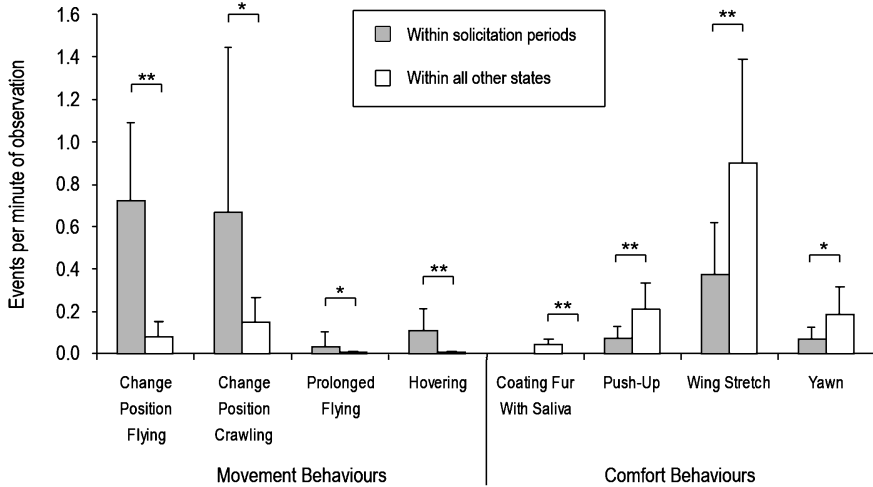
Figure 2. Incipient courtship behaviours (movement behaviours) occurred significantly more often during solicitation periods, whereas comfort behaviours were significantly more prevalent during other states. Means ± SD are shown. $^{*}p < 0.05$, $^{**}p < 0.0001$.

$p = 0.004, \alpha = 0.025$; phase 1: $91.9 \pm 7.1\%$, phase 2: $77.3 \pm 14.5\%$). The mean occurrence of incipient courtship behaviours (CPF, CPW, F, H) per minute of solicitation increased during ontogeny (Wilcoxon signed rank test, α adjusted according to sequential Bonferroni correction; $T = 2, N = 10$, exact $p = 0.006, \alpha = 0.05$; phase 1: 3.7 ± 2.8 events/m, phase 2: 7.1 ± 0.6 events/min), suggesting that solicitation periods became more complex as pups matured (Figure 3). The mean length of solicitation periods increased with increasing age of the pups (Wilcoxon signed rank test, α adjusted according to sequential Bonferroni correction; $T = 0, N = 10$, exact $p = 0.002, \alpha = 0.0167$; phase 1: 1.0 ± 1.0 min, phase 2: 5.8 ± 2.9 min; Figure 3).

Sex-specific behavioural differences

No significant differences between the sexes could be found for behavioural events or states (MANOVA with sex as fixed factor; events: $F_{1,16} = 1.272, p = 0.276$; states: $F_{1,16} = 1.139, p = 0.302$). This suggests that all behaviours observed were exhibited equally by both sexes. The increase in length and complexity of solicitation periods was not significantly different between male and female pups (Mann–Whitney U-test; $U = 7, N_1 = N_2 = 4$, exact $p = 0.886$; results identical for both length and complexity).
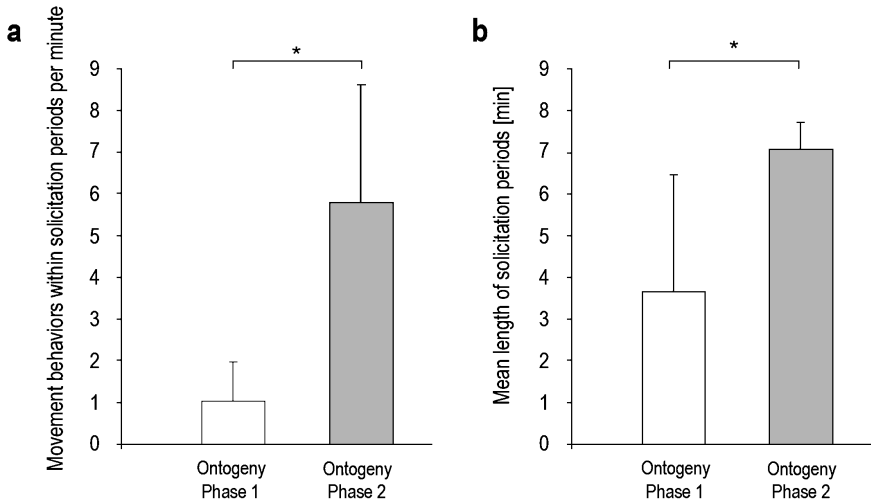
Figure 3. Solicitation periods became more complex (a) and longer (b) as pups matured. Both the mean occurrence of movement behaviours (incipient courtship behaviours) per min of solicitation and the mean length of solicitation periods increased significantly during ontogeny. Means ± SD are shown. $^*p < 0.05$.

Discussion

The daytime activity budget of *S. bilineata* pups is highly uncommon in bats (Jones, 2000; Kunz & Hood, 2000). Much of the pups' behaviour consisted of social interactions with the respective mothers through prolonged solicitation periods that became longer and more complex during ontogeny. The occasional aggressive termination of the solicitation attempts by mothers at a very early stage is distinctly different from the non-aggressive and either evasive or inviting behaviour of mothers during their pups' solicitation periods. Additionally, mothers regularly initiate solicitation periods by hovering in front of their young pups or by seeking physical contact with their pups. Therefore, prolonged solicitation periods cannot be attributed to a parent–offspring conflict over nursing alone (sensu Trivers, 1974).

In accordance with our first hypothesis, early ontogenetic expressions of adult male courtship occurred predominantly during solicitation periods, suggesting that solicitation periods might function as a trial ground for the practice of adult behaviours. In particular, hovering is a characteristic behaviour type that is both a frequently observed behaviour during solicitation periods and a stereotypic courtship display in adult males (Voigt & von

Helversen, 1999). We have anecdotal evidence that pups occasionally hover in front of vertical surfaces without the presence of roosting conspecifics, which further suggests that hovering is a manoeuvre that must be practiced. In contrast to nectar-feeding bats that are skillfull at hovering due to their foraging behaviour (Voigt & Winter, 1999), hovering in *S. bilineata* seems laborious and is considered to be energetically expensive (Voigt & von Helversen, 1999; Voigt et al., 2001). However difficult to define (Burghardt, 2005), 'play' in mammals can be considered behaviour types that occur outside of a clear functional context (Hass & Jenni, 1993; Spinka et al., 2001). This understanding of mammalian play applies to the behaviours of *S. bilineata* pups during solicitation periods, especially in regard to hovering. Play can be studied to understand the evolutionary forces that have shaped adult behaviour patterns (Fagen, 1981). In this context, the solicitation periods of *S. bilineata* pups may have a functional significance similar to play because physical strength, endurance and skill (the 'motor training hypothesis') can be developed during solicitation periods (Bekoff & Byers, 1981; Byers & Walker, 1995). For both male and female pups, enhancing fitness and agility would enhance their survival as adults. In a recent review of mammalian play, play is proposed as a rehearsal behaviour for unexpected events where the animal loses control over its sensory/spatial input, position or locomotion and needs to regain its control quickly (Spinka et al., 2001). Social interactions in adult *S. bilineata* can be highly aggressive, especially during courtship and male–male competition for access to females and harem territories (Bradbury & Emmons, 1974). The ability to recover from aggressive interaction is essential for survival in the colony, and training for these events may occur during ontogeny. Although the role of play in ontogeny as prefunctional adult behaviour has been debated, play is developmentally advantageous for a species that exhibits an abrupt developmental transition into adulthood when the behaviour pattern must be preformed adequately as soon as it is needed (Burghardt, 2005). This is relevant to *S.bilineata* because pups must serve as functional adults after weaning. *S. bilineata* pups may repeat behaviours through solicitation periods that are important for the acquisition of courtship competence. Adult *S. bilineata* males court females year-round (Voigt et al., 2008) and pups may modify their behaviours through the observation of adult male courtship behaviour. Moreover, pups might observe the hover flights of their mothers, which females perform when initiating solicitation periods. An alternative explanation for our findings would suggest that

the ritualized courtship observed in adult males develops from pup solicitation precursors. This is supported by the occurrence of courtship behaviours such as CPW, CPF and hovering, predominantly during the solicitation period. However, this explanation does not explain why solicitation periods in *S. bilineata* are so complex in comparison to other bat species (Jones, 2000; Kunz & Hood, 2000).

In contrast to our second hypothesis, sex-specific differences were neither found in the pups' overall behaviour nor in the length and complexity of solicitation periods. Sex-specific behavioural differences are most pronounced in adults, but these differences can normally be observed in juvenile animals as well (horses: Boy & Duncan, 1979; elephants: Lee, 1986; sheep: Hass & Jenni, 1993; monkeys: Eaton et al., 1986; Förster & Cords, 2005). Although the behaviour of male and female pups does not parallel the studies mentioned above, our findings are comparable to another study of *S. bilineata* (Knörnschild et al., 2006). This study reports that pups utter vocal renditions resembling the vocalizations of adult bats. These renditions are referred to as 'babbling' and may be used to encourage maternal care during solicitation attempts. The authors suggested that the pups babble to practice adult vocalizations. Although males carry out the majority of adult vocalization types (Behr & von Helversen, 2004), both sexes participate in practicing all vocalization types during ontogeny, including ones that are used exclusively during male courtship later in life (Knörnschild et al., 2006). It is hypothesized that female pups babble in order to create an acoustic template on which to base future mate choice decisions (Knörnschild et al., 2006). In male pups, the incipient courtship behaviours exhibited during solicitation periods could be considered a preparation for courtship. It might be possible that female pups practice the same behaviours to understand the energetic costs of male courtship, which are assumed to be considerably high (Voigt & von Helversen, 1999; Voigt et al., 2001). Through familiarity with the behavioural displays, females may be able to judge the performance of courting males.

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Appendix A

Videos (MPEG2, 512×382, 25.000 fps) were made in the bats' day-roosts with hand-held digital camcorders (Video 1: Sony Digital Handycam DCR-TRV10E PAL with infra-red light for illumination; Video 2: Canon Digital Camcorder MV900 with daylight for illumination).

Video 1. Excerpt from adult male courtship display. In the beginning, the courting male is on the right, the female on the left. Three different movement behaviours (hovering and changing position by crawling and flying) exhibited by the male are shown. The female remains mostly stationary during courtship. Odour presentation though salting, which is common during male courtship is not shown in this excerpt; however, odour presentation often occurs through hover displays as well. Video courtesy of Oliver Behr.

Video 2. Excerpt from pup solicitation behaviour. In the beginning, the soliciting pup is on the bottom right, its mother in the middle. On top is another female nursing her pup. Three different movement behaviours (hovering and changing position by crawling and flying) exhibited by the pup are shown. Note the overall similarity between adult male courtship display and pup solicitation behaviour.