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RISK-TAKING BY JUVENILE VERVET MONKEYS

by

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Summary

Because of their greater vulnerability to mortality, juveniles might be expected to be more conservative than adults in response to novel and potentially threatening situations. Results from research on vervet monkeys (*Cercopithecus aethiops sabaeus*) in the field and in captivity suggest that the opposite is true. Juveniles in the field were more likely to approach a human observer, and in captivity they had shorter latencies to enter a new area, approach a novel food container, and come within a meter of a strange adult male when compared to younger and older animals. In all four test conditions, risk-taking was an inverted U-shaped function of age. Latency to approach in unfamiliar and potentially dangerous situations declined from birth to two years of age, then increased with age to adulthood.

Introduction

The reaction of individuals to unfamiliar and potentially threatening situations has been studied as evidence of both species and individual differences in temperament (*e.g.* SCOTT & FULLER, 1965; REZNICK, 1989) and has been related to differences in physiology, genetics, dominance rank, and early experience (KATZIR, 1983; SUOMI, 1987; KAGAN *et al.* & 1988; LYONS *et al.*, 1988; FAIRBANKS, 1989; SIMPSON & DATTA, 1990; JONES *et al.*, 1991; SCHNEIDER *et al.*, 1991). From an evolutionary biological perspective, the initial response of an animal in unfamiliar situations would be expected to have important consequences for individual fitness. Too assertive a strategy in response to novelty can lead to injury or death,

while too conservative a strategy can lead to starvation or lost opportunity to acquire resources, mates, nest sites, or territory.

There are two contradictory themes in the current view of how age should influence response to unfamiliar and potentially threatening situations. From one perspective, there are reasons to expect juveniles to be cautious in unfamiliar situations when compared to older mature conspecifics. Among most animal species, juvenile mortality is high and only a small proportion of individuals survive to breeding age. Variability in the survival of juvenile offspring was found to be a major component of variation in lifetime reproductive success in longitudinal studies of great tits (VAN NOORDWIJK & VAN BALEN 1988), Florida scrub jays (FITZPATRICK & WOOLFENDEN, 1988), and red deer (CLUTTON-BROCK et al., 1988). Even among primates where both fecundity and mortality are low, juvenile mortality rates generally exceed those of adults (CHENEY & WRANGHAM, 1987). In a population of vervet monkeys at Amboseli National Park, for example, only 27% of all females born were estimated to survive to adulthood, and the proportion of variation in lifetime reproductive success explained by simply surviving to breeding age was greater than that explained by individual differences among adult breeders (CHENEY et al., 1988).

JANSON & VAN SCHAIK (1993) argue that juvenile primates have adopted a risk-averse strategy that involves seeking the close company of adults to minimize the risk of predation, but at the cost of increased competition for food. As a consequence, the slow growth rate and long period of development typical of juvenile primates (CASE, 1978) has evolved to reduce the chance of mortality due to malnutrition. There is evidence from the field that juveniles do maintain shorter inter-individual distances than older animals and are less likely to be seen alone (FAIRBANKS & BIRD, 1978; PEREIRA, 1988; VAN NOORDWIJK et al., 1993; STRIER, 1993). On the basis of this reasoning, juveniles would be expected to be more cautious than adults in approaching unfamiliar, potentially risky situations.

This view of the risk-averse juvenile is contradicted by our impression of juveniles as curious, playful, and exploratory (PEREIRA & ALTMANN, 1985). The juvenile period is often described as a time of enhanced receptivity for learning (POIRIER et al., 1978). Juvenile curiosity and will-

ingness to take risks in unfamiliar situations have been hypothesized to provide immediate benefits in terms of access to uncontested resources and also to create opportunities for learning that will enhance fitness later in life. Studies of juvenile primates have provided some support for this view by demonstrating that juveniles are more likely than adults to explore and manipulate non-threatening novel objects (MENZEL & MENZEL, 1979; JOUBERT & VAUCLAIR, 1986), and they are more likely to discover new foods or develop new food-handling methods (CAMBEFORT, 1981; NISHIDA, 1987).

This report documents developmental changes in the tendency of vervet monkeys to approach a novel and potentially threatening situation to determine whether juvenile vervet monkeys are more or less risk-averse than adults. Risk-taking was evaluated in four different test conditions, including habituation to a human observer, willingness to enter a new area, to approach a novel food container, and to come within a meter of a strange adult male. The results from all four test conditions indicate that risk-taking can be described as an inverted U-shaped function of age. Latency to approach in unfamiliar and potentially dangerous situations declines from birth to two years of age, then increases with age to adulthood.

Field observations on St. Kitts

In order to develop an index of relative visibility for forest living mangabeys, CHALMERS (1968) compared the likelihood of being sighted by a human observer with estimates of the proportion of different age-sex classes in a population. Similar data from a field study of socio-spatial behavior of free-ranging vervet monkeys on St. Kitts, West Indies (FAIRBANKS & BIRD, 1978), are used here to determine if here were age-related differences in the degree of avoidance of human observers. Vervet monkeys were considered an agricultural pest on St. Kitts, and were also hunted for food. As a result, the vervets were afraid of humans and their typical response to human intrusion was to alarm call and seek safety. Relative visibility can be used, therefore, as an index of the degree to which members of each age-sex class approached or avoided a potential threat.

Study site and methods

In 1974, a six month field study was conducted on a group of vervet monkeys (*Cercopithecus aethiops sabaeus*) that inhabited the area east of Timothy Hill on St. Kitts' southeastern peninsula. Most of the study area was covered with a continuous shrub layer, consisting primarily of *Acacia tortuosa*, a dense spiny shrub that varied in height from 5 to 10 ft, intermixed with a variety of other shrubs and trees. A dirt road transected the area, separating the acacia-covered hillside from a shallow lake and mangrove thicket.

In order to avoid modifying the monkeys' behavior as much as possible, the observer did not follow the monkeys, but instead, sat quietly at several observation posts along the day range of the group. The age-sex class, location, behavior and distance to nearest neighbor were coded for each monkey as they were sighted by the observer. Most animals were not recognized individually and were coded according to size class for immatures and sex for adults. The same individual was not intentionally recorded as a focal subject twice at the same location. After the troop had left the area, the observer moved ahead to the next observation post. One of the observation posts was at a road crossing. The animals usually arrived there mid-morning and would coalesce before crossing the road together. At this point complete counts of the troop were possible. (See FAIRBANKS & BIRD, 1978, for more detail of the study site and methods.)

Results

Comparisons of the proportion of each age-sex class in the scan samples and in the road crossing counts were used to estimate the relative visibility of each age-sex class to the human observer. The crossing counts indicated that the study group contained 1 adult male, 7 adult females, 10 juveniles, and 6 infants, with 4 additional adult males loosely associated with the group during the period of observation. Of the 1285 focal subject samples recorded for this group, 18% were on adult males, 22% on adult females, 45% on juveniles, and 15% on infants (Table 1). Thus, juveniles were overrepresented and adult females and infants were underrepresented in the samples relative to their numbers in the group (χ^2=53.71, df=3, p<0.01).

TABLE 1. Comparison of sightings of free-ranging vervet monkeys on St. Kitts by age-sex class with expected values based on road crossing counts

Age-sex class	Observed in scan samples N	Observed in scan samples %	Expected from crossing counts %
Adult male	230	18	18
Adult female	287	22	25
Juvenile	576	45	36
Infant	192	15	21

χ^2=53.71, df=3, p<0.001.

Several factors, such as larger size and greater disturbance of the vegetation, should have made adults more visible than juveniles. However, the results suggest that the behavior of the animals was a more important factor. The juveniles appeared more curious and were more likely to approach and vocalize in the presence of the observer, while adult females, particularly mothers carrying infants, stayed hidden and were more likely to avoid detection.

Captive challenge tests

To provide further evidence of the tendency for juveniles to approach novel and potentially dangerous situations, three different challenge tests were performed using socially-living animals of known age and identity under controlled conditions in captivity.

Subjects

Subjects for all three studies were monkeys living in four social groups at the Nonhuman Primate Research Facility at the Sepulveda Veterans Administration Medical Center. The colony, originally formed in 1975 with animals captured from St. Kitts, West Indies, has been maintained with the object of creating a relatively natural social environment within the constraints of captivity. Adult females and their immature offspring remain in their natal group, natal males are removed at 4-6 years of age, and breeding adult males are introduced and replaced at 3-4 year intervals. In order to maintain a group size of between 15 and 30 individuals, the original group was split into two in 1977, and into four in 1986.

Each group is housed in an octagonal-shaped outdoor enclosure, approximately 15 meters in diameter, with food and water continuously available.

Methods

Test 1: Latency to enter a new environment.

In January 1986, prior to the fission of two groups into four, tunnels leading from the two home enclosures were opened leading into newly constructed enclosures. The new enclosures were comparable in size and shape to the original enclosures, but they differed considerably in vegetation. Each had tall grass, bushes and two small trees. They also differed from the original enclosures in having a chain link roof and internal support posts. All of the juveniles and almost of the adults had never been outside of the enclosure where they were born. Latency to enter the new enclosures was used as a measure of willingness to explore a novel, and potentially dangerous physical space.

The test group tested was locked out of the night room so that all individuals had visual access to the 4'10" tunnel connecting the home enclosure to the new enclosure. The divider at the entrance to the tunnel was removed for the first time and the latency (in seconds) of each monkey to enter the new enclosure was recorded. Three observers worked together to record the latencies, and a videotape was used to verify times and animal identity. At the time of testing, the two groups contained 32 and 30 individuals, including a total of 5 adult males, 19 adult females, 12 juvenile males, 10 juvenile females, and 16 infants.

Test 2: Latency to approach a novel food source.

Prior observations in the captive colony and in the field suggested that vervet monkeys can be extremely wary of new food sources and even of familiar food found in novel places. The vervets on St. Kitts avoided familiar food items that had been moved to a new location, and in the colony, one of the captive groups had shown fear responses for several weeks when the old food bin had been first introduced eight years earlier. (FAIRBANKS, unpublished data). In May 1987, the old food bins that had been used for the prior eight years were replaced with new containers that differed in shape and surface material. The new bins were upright and had a shiny, reflective surface. The response of the monkeys to the new food containers was recorded to evaluate individual differences in the tendency to approach a novel and unfamiliar food source.

On the day of testing the new food container, containing monkey chow, was covered with a tarpaulin and placed inside the enclosure, in a location that differed from the typical placement of the old container. The cover was removed and three observers recorded the latency of each animal to approach within 1 meter of the new container. The four groups contained 24, 20, 19, and 16 animals respectively, including a total of 5 adult males, 21 adult females, 18 juvenile males, 18 juvenile females, and 17 infants.

Test 3: Latency to approach a strange adult male.

In the third challenge test in October 1990, a cage containing a strange adult male was placed at the periphery of the enclosure, and the latency for individuals to approach was recorded as a measure of risk-taking in response to an unfamiliar and potentially threatening conspecific.

An adult male unfamiliar to any of the study groups was placed in an individual cage (2'1" wide × 2'7" high × 2'3" deep) with open bars at the front and top and the covered cage was positioned adjacent to the chain link side of the study group. The cover over the cage was removed and the latency in seconds of each individual to approach within 1 meter of the cage was recorded. The four study groups contained 22, 25, 18, and 21 animals respectively, including 12 adult males, 23 adult females, 28 juvenile males, 15 juvenile females, and 8 infants.

Data analysis

For data analysis, each individual in the group was coded according to sex, age in months, and log latency. Individuals who never entered the new enclosure or approached within one meter of the test stimulus in the one hour test periods were assigned the maximum score. Young infants, under two months old, were all carried by their mothers throughout the test periods and were excluded from the analysis. Latencies for older infants refer to approaches by the infants themselves when they were not being carried by any other group members.

The effects of age and sex on approach latencies were tested by two-way analyses of variance with age grouped into 6 blocks: <12 months, 12-23 months, 24-35 months, 36-47 months, 48-71 months, and >72 months. When fitting the results to polynomial equations, age was coded to the nearest month for animals younger than 72 months, and as 72 months for older animals. The mean latencies and the pattern of results across groups were similar and the results have been combined for these analyses, except as noted below.

Results

Test 1: Latency to enter a new environment.

Opening the tunnel to the new enclosures produced immediate interest and excitement in both groups. In Group 1, the first individual to pass through the tunnel into the new enclosure was a 2-year-old female who entered in 12 second. In Group 2, a 2-year-old male entered first with a latency of 29 second. At the end of the 1 hour test sessions, all animals in Group 2, and all but 1 adult female from Group 1 had entered the new enclosure.

Figure 1 shows the relationship between age in years and latency to enter the new enclosure. Analysis of variance of latency by age and sex revealed a significant effect of age on latency to enter (F=3.69, p<0.01) but no effect of sex (F=0.00, p=.96) and no interaction of age by sex (F=1.77, p=0.14). Two-year-old juveniles had significantly shorter latencies than younger and older individuals.

A stepwise polynomial regression analysis was performed to verify the curvilinear nature of the relationship between age and response latency, and to identify the inflection point of the curve. The regression analysis
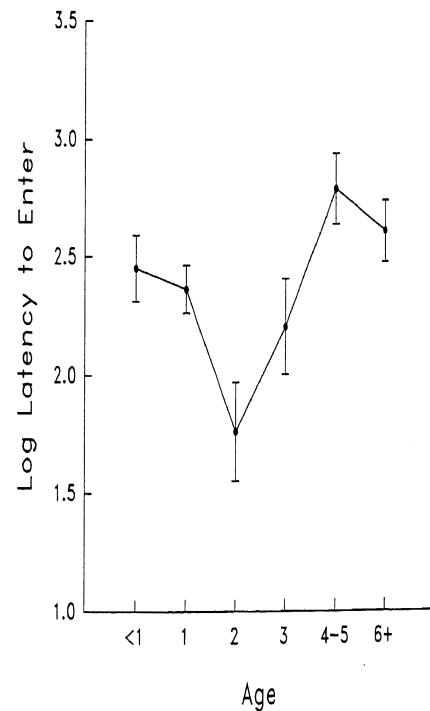

Fig. 1. Mean log latency in seconds (± s.e.m.) to enter the new enclosure by age in years.

predicting log latency to enter the new enclosure by months of life produced a negative first order coefficient and a positive second order coefficient, with the turning point at 30 months of age ($y = 2.86 + -.0545 \times \text{month} + 0.0009 \times \text{month}^2$) (multiple $r = 0.44$, $F = 9.33$, $p < 0.01$).

Test 2: Latency to approach a novel food source.

The vervets responded to the new food containers with interest and a combination of fear and attraction in each of the four groups. The first animal to approach within 1 meter was a 6-year-old male (Group 1, 15 sec.), a 2-year-old male (Group 2, 10 sec.), a 3-year-old female (Group 3, 6 sec.), and a 1-year-old male (Group 4, 17 sec.). The latencies were significantly longer for Group 1 than for the other three groups, and 3 adult females, one 8-month-old male, one 9-month-old female, and one 2-year-old female from this group never came within 1 meter of the new food container in the 1 hour test session. The other 3 groups did not differ in average latency, and every group member approached the new food container at least once, with the exception of one 2-year-old female in Group 2.

Figure 2 shows the relationship between age and latency to approach the novel food container. Analysis of variance of latency to approach within 1 meter of the new food container by age and sex revealed a significant effect of age ($F = 2.79$, $p = 0.02$) but no effect of sex ($F = 1.23$, $p = 0.27$) and no age $\times$ sex interaction ($F = 0.31$, $p = 0.93$). The age effect also held when the group difference was controlled ($F = 3.45$, $p = 0.01$). The pattern of results is very similar to that observed above in the latency to enter the new enclosures. Juveniles had shorter latencies to approach than either younger or older individuals.

Fitting the data to a polynomial regression produced an equation that was similar to the one found for the latency to enter the new enclosures, with a negative first order coefficient and a positive second order coefficient, and an inflection point at 32 months ($y = 3.16 + -0.063 \times \text{month} + 0.0010 \times \text{month}^2$) (multiple $r = 0.34$, $F = 6.24$, $p < 0.01$).

Test 3: Latency to approach a strange adult male.

All group members reacted to the presence of the stimulus male, particularly the adult males of the group who displayed to and threatened the
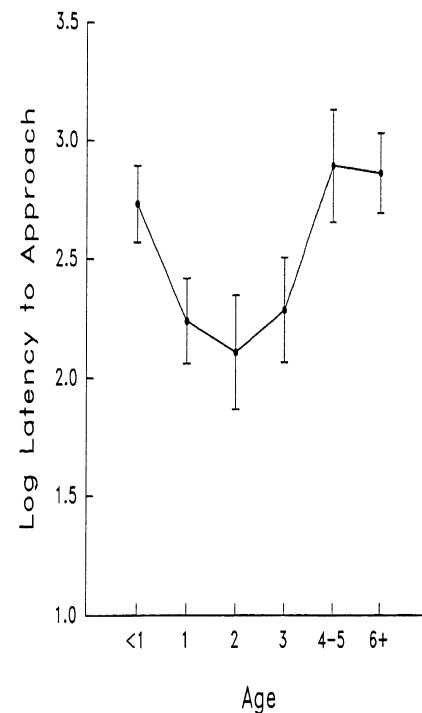

Fig. 2. Mean log latency in seconds (± s.e.m.) to approach within 1 meter of the new food container by age in years.

stranger. In spite of the high level of alarm exhibited by the adults, juveniles approached the cage with curiosity, showing relatively little fear. The first animal to approach the cage was a 3-year-old male in 3 of the 4 groups, and a 4-year-old male in the remaining group. In spite of this tendency for males to be first, was no significant effect of sex on latency to approach the stranger in the anova of age $\times$ sex ($F = 0.41$, $p = 0.52$). The reaction to the stimulus male was also similar in all four study groups and the average latency to approach did not differ by group ($F = 0.52$, $p = 0.67$).

The effect of age on the latency to approach the strange male was similar to that observed in the previous challenge tests ($F = 13.44$, $p < 0.01$) (Fig. 3). Infants and yearlings were more cautious than 2- and 3-year-olds who had the shortest latencies. The latency to approach increased with age from 3 years of age to adulthood. The adults, and particularly the adult males, all reacted to the strange male, but usually from a greater distance, and they had longer latencies to approach than did the juveniles. Of the seven animals who never approached to within 1 meter, three were adult males and 4 were adult females.
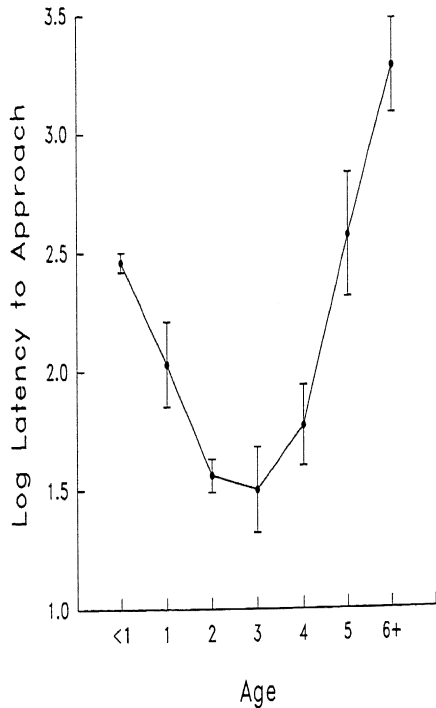
Fig. 3. Mean log latency in seconds (± s.e.m.) to approach within 1 meter of the strange adult male by age in years.

Polynomial regression analysis of latency by month of age produced a function that was similar to those found in the prior two tests with a negative first order component and a positive second order component and a minimum value at 34 months of age ($y = 3.72 + -.1366 \times month + .0020 \times month^2$) (multiple $r = 0.68$, $F = 41.67$, $p < 0.01$).

Discussion

Fearfulness and response to novelty has recently been a focus of attention in the field of child development (*e.g.* KAGAN *et al.*, 1987; REZNICK, 1989). The emphasis in this literature has been on fearfulness or 'behavioral inhibition' in response to novelty as a consistent personality trait that is genetically and physiologically based (KAGAN *et al.*, 1988; PLOMIN & STOCKER 1989). There is also evidence of consistent individuals differences in temperament along a comparable bold/fearful dimension in studies of nonhuman primates (SUOMI, 1987; FAIRBANKS & McGUIRE, 1988, in press; FAIRBANKS, 1989; SCHNEIDER *et al.*, 1991). Given the current focus on this dimension, it is particularly important to recognize

the maturational factors, both ultimate and proximate, that are involved in its behavioral expression.

Results from the field and from three different challenges in captivity all support the hypothesis that 2- to 3-year-old juveniles are more likely to approach a novel and potentially dangerous object or situation than are younger or older group members. The same pattern was observed in response to a human observer in the field, and to a new area, a novel food container, and a strange adult male conspecific in captivity. On an approach-avoidance dimension, juveniles were consistently less inhibited and more likely to approach in a novel situation that would be likely to involve risk to themselves.

These results are consistent with the view of juveniles as more curious and exploratory than adults. Prior studies of several different primate species have reported that juveniles are more likely than adults to explore and manipulate novel objects (MENZEL, 1969; MENZEL & MENZEL, 1979; JOUBERT & VAUCLAIR, 1986). Since the intention of these studies was to explore how monkeys form a cognitive map of their environment, the novel objects used were specifically selected to be non-threatening. The results of the present study suggest that the tendency for juveniles to respond to novelty also applies to situations that are potentially more dangerous.

While there are few data on the exact causes of mortality for juvenile primates, evidence from field studies of vervet monkeys suggest that the approach behavior shown by the juveniles in this study would be risky and could lead to an increased risk of injury or mortality. Leopards, the primary predator of vervet monkeys at Amboseli, are stealth hunters. They hide in bushes or in tall grass waiting to pounce on unsuspecting prey that enter the area (ISBELL, 1990). The tall grass and dense vegetation of the new enclosures easily could have provided a hiding place for a stealth predator. Hunting and trapping by humans is a significant mortality factor for vervets in the Caribbean (McGUIRE, 1974; HORROCKS & BAULU, 1988), and approach to a human observer, even one sitting quietly, is a risky behavior. While approaches to the new food containers might not seem very risky, this challenge test was chosen because the past behavior of the monkeys had indicated that they were wary of eating food found in unfamiliar places. The vervets on St. Kitts avoided familiar food items that had been moved to a new location (FAIRBANKS, unpublished

data), and in the colony, one of the captive groups had shown fear responses for several weeks when the old food bin had been first introduced eight years earlier. Finally, approaching within 1 meter of a strange adult male whose responses are unknown and unpredictable would seem to entail at least a certain degree of risk, particularly when the adult members of the group are exhibiting alarm behavior (HORROCKS & HUNTE, 1993). We do not know the exact risk that would be associated with these activities in a natural setting, but it is unreasonable to assume that there would be no risk.

The four test situations were varied but they all involved novelty, and the response of the juveniles was generally one of curiosity, not of confrontation. The juveniles exhibited a hightened sense of alertness as they approached the novel situations, and leapt away at the slightest stimulus, suggesting that they were aware of the risk and were ready to jump to safety. The relationship with age and the similarity of males and females found in these test situations would not necessarily by expected to generalize to risk-taking behaviors that involved more direct physical challenge, however. DALY & WILSON (1988) provide evidence for humans that the tendency to be involved in violent confrontations is much greater for males than for females, with a peak in late adolescence and young adulthood. The shorter approach latencies for juveniles reported here are likely to be a function of a differential response to novelty rather than a direct response to the level of risk.

Is the tendency for juveniles to approach in novel situations an adaptive response or is it an unavoidable byproduct of some other aspect of juvenile development? Many have speculated that by exploring unfamiliar aspects of the environment, a juvenile creates opportunities for learning which may enhance later fitness (PEREIRA & ALTMANN, 1985). The association of the extended juvenile period with large brain size and long life span is consistent with this view as both of these features have been associated with exploratory behavior and learning ability (GLICKMAN & SROGES, 1966; GOTTLIEB, 1992). There is also evidence that neural plasticity is greater prior to puberty than after (LENNEBERG, 1967), suggesting that there might have been selection for an augmented readiness to learn among juveniles compared to adults. Juveniles might also experience immediate benefits of risk-taking in unfamiliar situations if they can avoid competition with adults by being first. A juvenile who came across a new

food source might profit by eating first, before the arrival of older, larger group members (KATZIR, 1983). At this point, however, there has been little attempt to measure the fitness benefits of juvenile curiosity and risk-taking, and to determine whether the hypothesized benefits outweigh the cost of increased juvenile mortality (BEKOFF & BYERS, 1985). Considering the importance of surviving to adulthood in determining lifetime fitness, one would expect juveniles to be more conservative than they appear to be.

It is possible that the benefits of juvenile risk-taking do not outweigh the costs, but are the unavoidable consequence of other aspects of juvenile development. For example, the shorter latencies of juveniles could be a byproduct of their generally higher activity level. One of the leading hypotheses to explain why juveniles play argues that juveniles expend more energy than adults on seemingly unnecessary movement and activity because exercise promotes the healthy development of muscles and bones (BEKOFF, 1988). The general design of the juvenile brain-behavioral system appears to promote playful activity, and the shorter latencies of juveniles to approach a novel stimulus could be a consequence of this design (WOOD-GUSH & VESTERGAARD, 1991).

Another way to explain the juveniles' shorter latencies would be to postulate that they are cognitively unsophisticated and are not able to recognize or perceive the risks of their behavior. Or, they may have been less experienced and, as a result, less aware of the negative consequences of approaching. Data from vervet monkeys at Amboseli National Park suggest that competence in recognizing and giving appropriate species-typical vocalizations emerges gradually over the first three years of life (SEYFARTH & CHENEY, 1986; HAUSER, 1988). These results are consistent with the view that cognitive maturation and accumulated experience may determine the juvenile's ability to recognize the level of risk in a situation and thus influence the level of caution expressed. By this view, juvenile curiosity is not directly adaptive but is the unavoidable consequence of a slowly developing nervous system.

One particularly interesting aspect of the results presented here was the nature and consistency of the curves of approach latencies by age. How universal is the U-shaped curve, and what causes latencies to decline and then increase with age? Further study of the individual differences in approach latencies within age classes suggests that the exploratory behav-

ior of infants less than 1 year of age is controlled by their mothers (FAIRBANKS & McGUIRE, in press). The protective concern of the mothers declines with age and the juveniles appear to be free to act on their own. The increase in latency as animals mature to adulthood is more difficult to explain. Females may become responsible for dependent offspring, Thus contributing to their reasons for being cautions, but increased cautiousness was also found for males and for females without infants.

Returning to the question of the degree to which juveniles can be characterized as risk-taking or risk-averse, the answer must be both. While juveniles seek the proximity of adults for safety, they are also apparently more willing to expose themselves to risk in return for opportunities to enlarge their experience of the world. More research is needed to define the types of risk-taking behaviors that are characteristic of different life stages, and the real challenge will be to develop means of measuring the costs and benefits of these behaviors for the individuals involved.

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OVIPOSITION BEHAVIOUR OF DIPHAGOUS PARASITOIDS (HYMENOPTERA, APHELINIDAE): A CASE OF INTERSEXUAL RESOURCE PARTITIONING?

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Summary

Female diphagous parasitoids are endoparasitic as larvae, whereas their males are ectoparasitic. It is possible that males, during their development, eliminate competitors, and this has been proposed as the selective advantage to male ectoparasitism. In this way resources would be partitioned between the sexes. The hypothesis was tested experimentally by observation of whether mated females were capable of recognizing parasitized hosts, and whether they then deposited male eggs on them (because ectoparasitic larvae are supposed to be good competitors). The behaviour of individual *Coccophagus bartletti* ANNECKE & INSLEY (Aphelinidae) wasps did not follow prediction, and an alternative hypothesis is proposed. Selection pressures from the environment (*e.g.* host) need not be the same for both sexes, and if male eggs of the pre-diphagous aphelinid were treated differently at oviposition from female eggs (as is found in at least one extant species of aphelinid with otherwise conventional host relationships), a host shift at speciation could account for the divergence in host relationships of the sexes.

Introduction

Some parasitoids in the chalcidoid family Aphelinidae are well known because males of the species have host relationships that are quite different from those of their conspecific females. Such sex-related host associations are called heteronomous host relationships (WALTER, 1983a), and in the Aphelinidae they are restricted to species in a group of about eight