



Cultural differences in army ant predation by West African chimpanzees? A comparative study of microecological variables

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(Received 21 September 2007; initial acceptance 12 November 2007;
final acceptance 18 January 2008; published online 28 April 2008; MS. number: 9519)

Behavioural diversity in the predation pattern of army ants (*Dorylus* spp.) by different populations of wild chimpanzees, *Pan troglodytes*, has been proposed to reflect different cultural traditions. Chimpanzees use either stick tools (known as ant dipping) or simply their hands to prey on two groups of army ants (epigaic and intermediate species). A recent analysis has shown that, contrary to the cultural hypothesis, the tool length and associated harvesting technique used by chimpanzees in different populations is to a large extent influenced by characteristics of the ants themselves. However, in line with the cultural hypothesis, chimpanzees at two long-term study sites in West Africa (Bossou, Guinea, and Taï National Park, Côte d'Ivoire) prey on the same five army ant species but adopt different strategies to do so. We conducted controlled human simulations of ant dipping and an ant survey at these two sites to evaluate alternative ecological explanations related to ant behaviour and ecology that could account for the observed differences in chimpanzee predation behaviour. Ant speed explained differences in tool length within Bossou but not between Bossou and Taï. Our results do not support an ecological basis underlying the lack of dipping at ant trails in Taï chimpanzees. Finally, neither ant aggressiveness (measured as speed and persistence) nor yield when using tools could explain why, unlike Bossou chimpanzees, Taï chimpanzees do not use tools to harvest epigaic species. We conclude that an interaction of cultural and ecological factors shapes the differences in army ant predation between Taï and Bossou chimpanzees.

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Keywords: ant dipping; army ants; chimpanzee; culture; *Dorylus* spp.; insectivory; *Pan troglodytes verus*; tool use

It is widely acknowledged that different animal taxa such as chimpanzees, *Pan troglodytes*, cetaceans and orangutans, *Pongo pygmaeus*, possess population-specific behavioural traditions termed culture (Whiten et al. 1999; Rendell & Whitehead 2001; van Schaik et al. 2003). Culture is thereby broadly defined as a population-typical behaviour that is at least partly acquired and transmitted

through mechanisms of social learning (McGrew 1998; Laland & Hoppitt 2003). Detection of cultural transmission in wild animals is difficult, but one way of investigating the existence of culture is through the so-called method of exclusion or geographical method (Whiten et al. 1999; van Schaik et al. 2003). That is, a behaviour is customarily shown in one population but nonexistent in another population of the same species living in a similar environment such that an ecological basis for the difference can be excluded, and the behaviour is thus assumed to be the product of cultural transmission. This approach has been criticized by some and the debate is ongoing (Tomasello 1990; Laland & Janik 2006, 2007; Krützen et al. 2007). One prime example of a potential

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cultural behaviour that is regularly cited by supporters as well as opponents of the method of exclusion is the predation on army ants (*Dorylus* spp.) by wild chimpanzees.

Dorylus army ants are characterized by obligate collective foraging, and they regularly migrate to new underground nests (Gotwald 1995; Schöning et al. 2005a). The *Dorylus* species preyed on by chimpanzees have a nonfunctional sting, but fiercely defend their nests against predators by painful bites (Schöning et al., in press). They can be categorized into two groups: the epigaeic species which hunt more conspicuously above the leaf litter and in the vegetation and are very aggressive; and the intermediate species which hunt only in the leaf litter, are less conspicuous and retreat quickly upon disturbance (Schöning et al. 2005b).

Chimpanzees from five populations across Africa have been directly observed to prey on army ants, and there is indirect evidence (abandoned tools and faecal remains) of army ant consumption by chimpanzees at 12 additional sites covering all four subspecies (reviewed in Schöning et al., in press). When preying on army ants, chimpanzees either directly reach with one hand into the nest to retrieve the brood (eggs and larvae) from the nest cavity or they use thin, straight stick tools to collect adult ants from ant nests or trails. These tools are freshly manufactured from the surrounding vegetation and the tip of the tool is held among the mass of ants. When enough ants have attacked the tool, the chimpanzees either pull the length of the tool through the fingers of one hand, thus bringing the ants to their mouth (at Gombe, Tanzania, McGrew 1974) or they consume the ants either by sweeping the tool sideways through the mouth (at Bossou, Guinea, Sugiyama et al. 1988; Sugiyama 1995) or by inserting the tip of the tool into the mouth (at Tai, Côte d'Ivoire, Boesch & Boesch 1990). This harvesting technique with tools has been termed ant dipping (McGrew 1974). After comparing ant-dipping techniques between Tai where chimpanzees exclusively use the one-handed, direct-mouthing technique and Gombe where chimpanzees almost only use the two-handed, pull-through technique, Boesch suggested ant dipping is a cultural behaviour (Boesch & Boesch 1990; Boesch 1996). Recent data from Bossou showed that chimpanzees from the same population regularly use both techniques (Humle & Matsuzawa 2002; Yamakoshi & Myowa-Yamakoshi 2004). In addition, Humle & Matsuzawa (2002) showed that chimpanzees use longer tools for epigaeic species than for intermediate ones at ant nests (reanalysed in Schöning et al., in press). Furthermore, they established a link between tool length and subsequent harvesting technique, thus giving support to Sugiyama's (1995) suggestion that chimpanzee behaviour is an adaptation to prey behaviour. The association between tool length and prey characteristics was also found in a study comparing dipping tools and army ant identity across five chimpanzee populations covering the whole range of chimpanzee distribution (Schöning et al., in press). These results call into question whether the differences in army ant predation observed between chimpanzee populations are really cultural and are not due to differences in prey ecology.

Schöning et al. (in press) also found that the same five army ant species occur at Bossou and Tai. Three of these show the epigaeic lifestyle, the other two the intermediate one. Chimpanzees at both sites prey on all five species, but there are some major differences in predation strategies between the two populations (Schöning et al., in press). This raises the question whether other ecological differences between the two sites could explain the observed differences in chimpanzee predation behaviour or whether they are indeed cultural. Even when the same prey species is being targeted, intraspecific geographical variation in the prey's behavioural response might lead to differences in the predator's behaviour. We thus designed a comparative study between Bossou and Tai to investigate whether ecological variation, in this case the behaviour and availability of the ants, causes the following three major differences in army ant consumption between the two populations: (1) tool length; (2) whether intermediate ants are preyed on at trails; and (3) predation patterns on epigaeic ants.

Variation in Tool Length

Chimpanzees at Tai use short tools (mean length = 23.9 cm), dip only for intermediate ants and only at nests (Boesch & Boesch 1990), whereas Bossou chimpanzees, when dipping at nests, use long tools (mean = 74 cm) for epigaeic ants and shorter tools (mean = 56.5 cm) for intermediate ants (Humle & Matsuzawa 2002; Schöning et al., in press).

Schöning et al. (in press) found that epigaeic ants have longer legs than intermediate ones. They suggested that epigaeic ants could therefore run faster than the latter, forcing chimpanzees to use longer tools when dipping epigaeic ants to avoid being bitten. However, this inference has not yet been tested. We thus tested the prediction that epigaeic species run significantly faster than intermediate species.

Tai chimpanzees use significantly shorter tools when dipping for intermediate ant species at nests than Bossou chimpanzees (Schöning et al., in press). If intermediate species at Tai ran up the length of the tool more slowly than at Bossou, Tai chimpanzees could afford to use shorter tools. Assuming that the differences in tool length are caused by variation in the behaviour of the ants, we therefore predicted that intermediate species at Bossou would run faster than the same species at Tai.

Foraging at Trails

Chimpanzees at Tai have never been seen dipping for intermediate species at trails (Y. Möbius & C. Boesch, personal observation; Fig. 1), whereas at Bossou, chimpanzees dip at trails as well as nests (Sugiyama 1995; Humle & Matsuzawa 2002). If trails of intermediate ants were much less common at Tai than at Bossou, this might explain why Tai chimpanzees do not exploit trails. We thus predicted that trails of intermediate species would occur at lower densities at Tai than at Bossou.

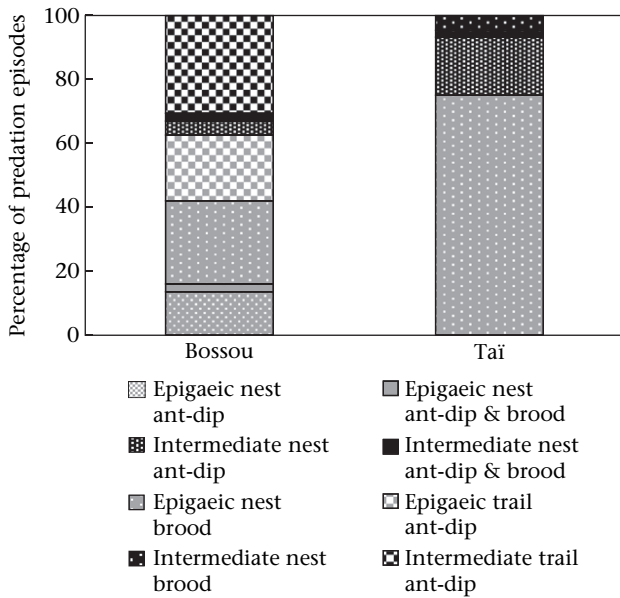


Figure 1. Percentage of predation episodes (ant dipping and brood extraction) recorded at nests and trails on both epigaeic and intermediate species at Tai ($N = 44$) and Bossou ($N = 88$), respectively.

Variation in Foraging on Epigaeic Ants

At Tai, in over 30 years of observation, only one adolescent female was ever seen to use a tool briefly to dip for an epigaeic species (Boesch & Boesch 1990), but Tai chimpanzees do manually extract brood from nests of epigaeic species (Fig. 1). At Bossou, chimpanzees dip with tools both at nests and trails of epigaeic species as well as take brood from these ants' nests (Humle & Matsuzawa 2002; Fig. 1). Although the proportion of predation events on epigaeic species is about the same in both populations, Tai chimpanzees eat solely brood and thus consume relatively more brood than Bossou chimpanzees (Fig. 1).

Such variation may be caused by the epigaeic army ants being more aggressive at Tai than at Bossou, such that using tools to dip would be too costly at Tai. If epigaeic species ran up the dipping tool faster at Tai and attacked more persistently than at Bossou, Tai chimpanzees would be forced to interrupt their dipping more often, use longer tools than Bossou chimpanzees or decrease the time the tool is held among the ants to avoid getting bitten, which would in turn result in decreased yield. We thus predicted that epigaeic species would run faster and attack more persistently at Tai than at Bossou.

Alternatively, if colonies of epigaeic ants at Tai were smaller or the ants clumped less at the nest entrance and stuck together less when being dipped, this would result in lower yield at Tai than at Bossou when using a tool and it might not be worthwhile for Tai chimpanzees to dip at either nests or trails of epigaeic species at Tai. We therefore predicted that yield from dipping epigaeic species would be lower at Tai than at Bossou.

Finally, army ants often build their nests at the base of trees such that the nest entrance is blocked by roots, making it difficult or impossible for a predator to retrieve brood from the nest cavity. If at Tai, nest entrances were

less often blocked by roots than at Bossou, it would allow Tai chimpanzees to focus on consuming brood rather than dipping with tools, as harvesting brood from nests by hand may be more efficient in terms of energy intake per unit time than dipping with tools (Boesch & Boesch 1990). We consequently finally predicted that the proportion of nests blocked by roots would be lower at Tai than at Bossou.

Testing Ecological Explanations

We conducted controlled human simulations of ant dipping (sensu Humle & Matsuzawa 2002) at both sites to measure different variables reflecting the behaviour of the ants (speed, persistence and yield), in two different contexts, nests and foraging trails, on all five species. In addition we compared nest structure and undertook surveys of the availability of ant colonies at both sites. Such a systematic approach allowed us to test ecological versus cultural explanations for army ant consumption behaviour at two long-term chimpanzee field sites in West Africa; Table 1 summarizes the predictions given above.

METHODS

Study Sites

The field site of Bossou ($7^{\circ}39'N$, $8^{\circ}30'W$) is situated in southeastern Guinea at the foot of the Nimba Mountains close to the borders of Liberia and Côte d'Ivoire. One community of chimpanzees at the Bossou research site has been habituated and studied since 1976. Their home range is dominated by secondary and scrub forest including a small area of primary forest. For further details of this field site see Sugiyama (1999) and Humle & Matsuzawa (2001, 2004).

The Tai Chimpanzee Project ($5^{\circ}50'N$, $7^{\circ}21'W$) was established in 1979 in the west of Tai National Park, Côte d'Ivoire, which covers an area of 4500 km^2 of

Table 1. Summary of predictions of ecological explanations for observed variation in chimpanzee behaviour and results

Predictions	Results
Tool length	
Epigaeic species run faster than intermediate species	Supported
Intermediate species run faster at Bossou than at Tai	No support
Foraging at trails	
Trails occur at lower density at Tai than at Bossou	No support
Foraging on epigaeic species	
Epigaeic species run faster and attack more persistently at Tai than at Bossou	No support
Yield from dipping epigaeic species is lower at Tai than at Bossou	Opposite effect
Proportion of ant nests blocked by roots is higher at Bossou than at Tai	No support

primary rainforest. Habituation of North community was complete by 1984 and of South community by 1995. Almost daily observations of both communities have been ongoing since. For more information about this field site see Boesch & Boesch-Achermann (2000).

Experiments Measuring Ant Behaviour

General procedure

We conducted two types of experiment with humans simulating ant dipping to measure the ants' defence behaviour and the yield gained from dipping (adapted from Humle & Matsuzawa 2002). Exactly the same protocol and procedures were followed at Tai and Bossou. The same plant species, *Glyphaea brevis* (Tiliaceae), was used to manufacture dipping tools at both sites. A fresh tool was used for every dipping session. Tools were 50 cm long and 5 mm in diameter. All sessions were filmed with a Sony DCR TRV 900E digital camera at Tai and with a Sony DCR TRV 20 digital camera at Bossou. Experiments at Tai were conducted in June 2006 and at Bossou from June to August 2006. Ant samples were collected from all experiments. Identifications of ant species were carried out by T.H., K.K. and Y.M. in the field and were later checked by C. Schöning, who is currently working on a taxonomic revision of the subgenus *Dorylus* (*Anomma*). The initial aim was to conduct experiments on five different colonies per ant species under each ant condition, that is, nest and foraging trail. We found nests by following the trails of ants that we encountered during our walks on forest paths in the chimpanzees' home ranges. Since trails of intermediate ants were rarely encountered at both locations, and owing to the ants' inconspicuous nature, we were unable to uncover five colonies for each of those species. Therefore we could not conduct enough experiments with the two intermediate species at both sites to allow for statistical analyses (Table 2). For various reasons (time constraints, illness of researchers, misidentification of ant species in the field, and loss of ant colonies that moved to a new nest) we also did not meet our intended sample size for the epigaecic species and sampled some colonies only in the foraging condition or only at the nest (Table 2).

Experiment measuring speed

The speed with which the ants run up the dipping tool is a direct measure of their readiness and ability to attack intruders. The faster they run the sooner they will reach the chimpanzee's hand and bite, thus forcing chimpanzees to use longer tools (or use shorter dip durations which might lower yield). For the experiment, two markings were carved into the dipping tool at 10 and 30 cm from the distal end of the tool. The tip of the tool was held at a 45° angle into the mass of ants, and ants were filmed running up the tool. Once several ants had passed the second marking the tool was withdrawn, shaken to remove ants and replaced among the ants for a new dip. Up to 20 dips were made and filmed during each session. Videos of the experimental sessions were digitized and coded by Y.M. using the software Interact Version 7.0 (Mangold

Table 2. Summary of number of trials (corresponding to different colonies) undertaken for each ant species at Bossou and Tai

Species	Bossou			Tai		
	Nest & Trail trail	Nest only	Nest only	Nest & Trail trail	Nest only	Nest only
Yield						
Epigaecic						
<i>Dorylus nigricans</i>	6	2	2	5	—	—
<i>Dorylus mayri</i>	4	1	1	5	—	—
<i>Dorylus burmeisteri</i>	4	1	1	5	—	—
Intermediate						
<i>Dorylus emeryi</i>	—	1	2	—	2	—
<i>Dorylus gerstaeckeri</i> complex sp. 1	—	2	1	—	1	2
Speed						
Epigaecic						
<i>D. nigricans</i>	5	1	2	4	2	—
<i>D. mayri</i>	4	2	1	5	—	—
<i>D. burmeisteri</i>	4	1	1	4	—	—
Intermediate						
<i>D. emeryi</i>	—	1	2	—	1	—
<i>D. gerstaeckeri</i> complex sp. 1	—	1	1	—	1	2

International GmbH, Arnstorf, Germany). The time it took the first ant of each dip to run from the first to the second marking, that is, a distance of 20 cm, was measured. For each experimental session, we coded the first 10 dips for which this was possible and included them in the analyses. Dips were excluded from the coding process when there was uncertainty as to when the first ant crossed the first or second marking. Ten randomly chosen dips were recoded by a second person who was not familiar with the study for a reliability test. The interobserver reliability of speed measurements (duration measured in seconds divided by 20 cm) was excellent (Spearman rank correlation: $r_s = 0.987$, $N = 10$, $P < 0.001$).

Experiment measuring persistence and yield

We used the change in number of ants harvested per dip during a dipping session as a measure of the ants' persistence in attacking intruders. An increase or no change with increasing dip order indicated the ants' continued readiness to attack the intruding object, whereas a decrease indicated lower persistence. An increase would imply a higher risk for chimpanzees of getting attacked and bitten during a dipping session.

Yield is a direct measure of the chimpanzees' reward when dipping. It probably depends on the number of ants in the nest, how much they clump at the nest entrance and how much they stick together when being dipped. During the experiment conducted to measure yield and persistence of ants, one person dipped by holding the tool at a 45° angle among the ants, making slight regular back and forth movements with the tool to stimulate the ants to attack the tool similar to the method used by Bossou chimpanzees. One experimental session was conducted with each colony in each condition. Each of these dipping

sessions consisted of 32 consecutive dips. To simulate the range of variability seen in dipping by chimpanzees, we used four different dip durations (time the tool was in contact with the ground and ants) of 2, 4, 6 and 8 s each. The protocol of one session comprised eight sequences of these four dip durations in a randomized order. One experimenter followed the pre-established sequence and called out dip durations to the person dipping. Dips were separated by 20 s intervals from the time the tool lost contact with the ground to the moment it was replaced. Within these 20 s we gathered all ants from the tool into sealable plastic bags for counting. Each dipping session lasted 13 min.

Survey of Ant Availability and Nest Structure

To estimate the availability of colonies of the ant species of both lifestyles, we undertook an ant survey by walking along forest paths in the chimpanzee territories at both study sites (two territories at Tai, one at Bossou) and counted all foraging trails, migration trails and swarm raids of ants that we encountered on the path. These forest paths were evenly distributed throughout both home ranges at Tai and the chimpanzee home range at Bossou and included almost all existing paths. Forest paths look similar at both sites and visibility conditions did not differ between the two sites personal observation (Y. Möbius, personal observation). The distance covered (measured with pedometers) was 20 km at Bossou and 53 km at Tai. Samples were collected from all ants encountered; identification was done in the field by T.H., K.K. and Y.M. and later checked by C. Schöning.

Statistical Analysis

Since we did not have data on chimpanzee predation behaviour at the species level at Tai, and chimpanzees clearly differentiate between lifestyles when foraging on army ants, we pooled data on different species within a given lifestyle to test for differences between sites and ant condition (nest or trail). To compare the speed of ants of the epigaecic and intermediate lifestyles, ant species were pooled within lifestyles at each site under each ant condition and then compared with Mann–Whitney U tests to calculate exact P values. Spearman correlation coefficients were calculated to evaluate the effect of dip order on the number of ants harvested per dip. To control for potential effects of dip duration we also calculated the partial correlations between dip order and the number of ants harvested (control variable: dip duration). Since ordinary and partial correlation coefficients were highly correlated (Spearman rank correlation: $r_s = 0.947$, $N = 58$, $P < 0.001$), we used the bivariate correlation coefficients in a repeated measures analysis of variance (ANOVA) to test whether they differed between ant condition and sites. We ran this analysis including all 28 within-colony experimental sessions conducted at foraging trails and nests at Bossou and all 30 sessions at Tai.

Similarly, we used repeated measures ANOVAs to investigate the effect of study site (between-subjects factor)

and ant condition (within-subjects factor), that is, foraging trail or nest, on speed of ants and yield from experimental sessions with epigaecic species. When there was a significant interaction between two factors, the results for the single factors were established as not reliable (Zar 1999) and therefore we do not report them. In these cases data were split between sites and/or condition to investigate further the nature of the interaction. We used paired t tests to test for an effect of ant condition separately for both sites and Student's t tests for tests of a site effect within ant condition. In repeated measures ANOVAs testing for a difference between nests and trails of epigaecic species we included only colonies that we had sampled under both conditions (Table 2). In analyses run separately for foraging trails and nests testing for a site or lifestyle effect we included all sessions to increase our sample size. We visually checked for homoscedasticity of variances in all ANOVAs by plotting residuals against expected values. Whenever error variances were not equally distributed, we transformed the data using the natural logarithm. This improved the distribution of variances. For all tests we used SPSS version 13.0 (SPSS Inc., Chicago, IL, U.S.A.). All tests were two tailed, except for the binomial probability test used to compare foraging trail densities of intermediate species at Bossou and Tai. As we covered different distances at the two sites, the expected values had to be corrected for sampling effort. In such cases, the sampling distribution is asymmetric, and it is only possible to carry out one-tailed tests. Effect sizes indicated are partial eta-squares (η^2).

RESULTS

Variation in Tool Length

As predicted (Table 1), epigaecic (E) ants were significantly faster than intermediate (I) ants at nests and trails at both sites (Mann–Whitney U test: Bossou: foraging trail: $U = 0$, $N_E = 17$, $N_I = 2$, $P = 0.012$; nest: $U = 0$, $N_E = 17$, $N_I = 3$, $P = 0.002$; Tai: foraging trail: $U = 0$, $N_E = 15$; $N_I = 2$, $P = 0.015$; nest: $U = 0$, $N_E = 13$, $N_I = 2$, $P = 0.019$; Fig. 2). This may explain why Bossou chimpanzees use longer tools when dipping at nests for the faster epigaecic species than for the slower intermediate ones, and why Tai chimpanzees, who dip only for the slow intermediate species, use short tools.

Owing to small sample sizes, we could not statistically test whether intermediate ants at nests ran faster at Tai than at Bossou as predicted under the ecological hypothesis. Visual inspection of the data shows, however, that their speed was in the same range at both sites (Fig. 2) and indicates that there is at least no biologically meaningful difference between sites to explain why Tai chimpanzees use significantly shorter tools than Bossou chimpanzees when dipping for intermediate species at nests.

Foraging at Trails

Our data on density do not support the prediction that trails of intermediate ant species are less available at Tai, as

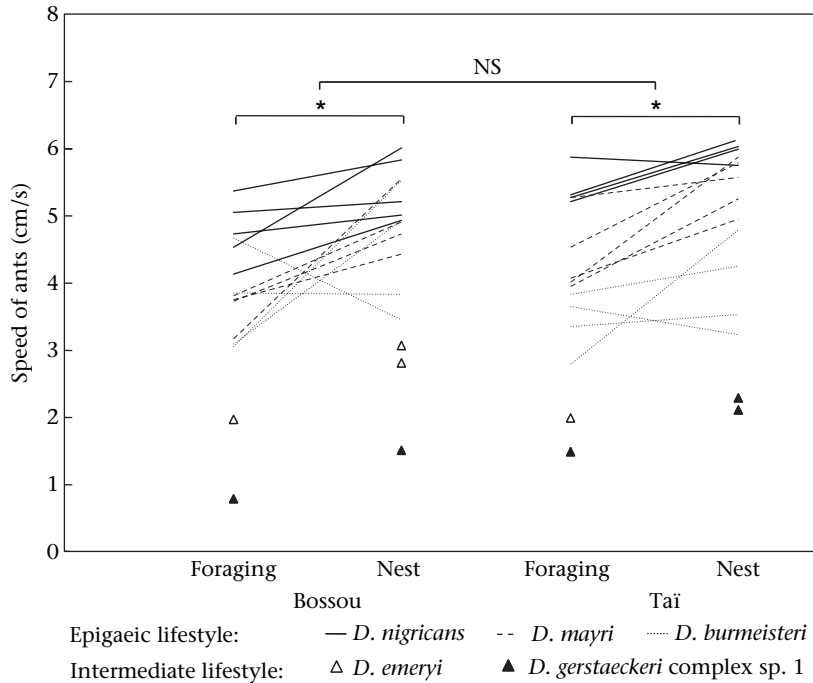


Figure 2. Mean speed per session of ants running up the dipping tool at Bossou and Taii under two different conditions, nest and foraging trail, for each species (repeated measures ANOVA of epigaecic species: $*P < 0.001$; NS: $P = 0.564$; within-colonies design for epigaecic and between-colonies design for intermediate species).

density of trails was the same at Bossou (B) and Taii (T) (binomial probability test: $N_B = 2$, $N_T = 9$, one-tailed $P = 0.384$). A lack of opportunity is thus not the reason why Taii chimpanzees do not dip at trails of intermediate species.

Variation in Foraging on Epigaecic Ants

Epigaecic ants ran up the dipping tool faster at nests than they did at trails. No difference in speed of the ants was observed between sites (repeated measures ANOVA: nest versus foraging trails: $F_{1,24} = 18.577$, $P < 0.001$, $\eta^2 = 0.436$; site: $F_{1,24} = 0.342$, $P = 0.564$, $\eta^2 = 0.014$; interaction condition*site: $F_{1,24} = 0.302$, $P = 0.588$, $\eta^2 = 0.012$; Fig. 2). Moreover, for epigaecic species, the number of ants harvested per dip decreased at both sites with increasing dip number at foraging trails, but not at nests (Table 3). Despite this difference between nests and trails there was no difference in persistence of the ants between Bossou and Taii (nest versus foraging trails:

$F_{1,27} \leq 30.604$, $P < 0.001$, $\eta^2 = 0.531$; site: $F_{1,27} = 1.103$, $P = 0.303$, $\eta^2 = 0.039$; interaction condition*site: $F_{1,27} = 1.663$, $P = 0.208$, $\eta^2 = 0.058$). Thus, we did not find any differences in aggressiveness of ants as measured by speed or persistence of defence that could explain why, unlike Bossou chimpanzees, Taii chimpanzees do not dip epigaecic species.

Furthermore, in an overall analysis of yield per dipping session, the difference in yield between foraging trails and nests was larger at Taii than at Bossou (interaction condition*site: $F_{1,27} = 5.875$, $P = 0.022$, $\eta^2 = 0.179$). In separate analyses for each site, yield was significantly greater at nests than at foraging trails at both sites (paired t test: Bossou: $t_{13} = 5.67$, $P < 0.001$; Taii: $t_{14} = 7.82$, $P < 0.001$). We found no difference in yield between the two sites at foraging trails, but, contrary to the prediction from the ecological hypothesis, yield at nests was significantly greater at Taii than it was at Bossou (Student's t test: foraging trail: $t_{32} = 0.43$, $P = 0.67$; nest: $t_{31} = 3.69$, $P = 0.001$; Fig. 3).

Table 3. Summary statistics of Spearman correlation coefficients (r_s) of number of ants harvested per dip with increasing dip order for epigaecic species

Site	N	Mean r_s	Range	SD	P
Foraging trail					
Bossou	14	-0.547	-0.845--0.309	0.177	<0.001
Taii	15	-0.367	-0.892--0.209	0.345	0.001
Nest					
Bossou	14	-0.097	-0.413--0.403	0.272	0.207
Taii	15	-0.087	-0.771--0.495	0.361	0.366

The P values were derived from one-sample t tests of the null hypothesis that mean $r_s = 0$.

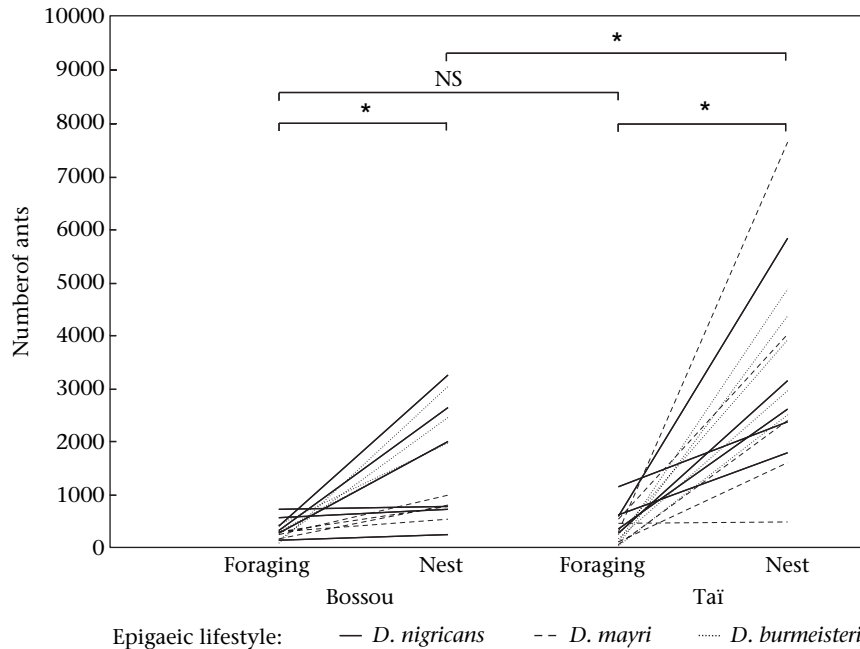


Figure 3. Total yield per dipping session at Bossou and Taii under two different ant conditions, nest and foraging trail, for each species (paired and Student's *t* tests: * $P < 0.01$; NS: $P = 0.67$).

Finally, the proportion of nests with roots (scored as present or absent) covering the nest entrance and thus potentially hampering access to the brood did not differ between Bossou and Taii (Bossou: $N_{(\text{no roots}/\text{roots})} = 15/3$; Taii: $N_{(\text{no roots}/\text{roots})} = 17/4$; Fisher's exact test: $P = 1$). Thus, nest structure also did not explain why Taii chimpanzees do not use tools to harvest epigaeic ants.

DISCUSSION

The results of our experimental study support one ecological prediction regarding the observed variation in chimpanzee ant dipping within Bossou, namely that epigaeic ants run faster than intermediate ones (Table 1). However, of the three major differences in army ant predation between Bossou and Taii that we investigated, that is, tool length, whether intermediate ants are preyed on at trails or not, and predation patterns on epigaeic ants, we found no support for predictions of microecological variation causing the observed differences between the two populations.

Epigaeic ants ran up the dipping tool twice as fast as intermediate ants, supporting inferences based on morphology (Schöning et al., in press). This implies that for the same dip duration the minimum tool length required when dipping for epigaeic ants is twice that for intermediate ones. Speed of the ants hence explained the observed differences in tool length used by chimpanzees at Bossou when dipping for ants of different lifestyles at nests. It also explained why Taii chimpanzees, who dip only for intermediate species at nests, use short tools. However, our results did not indicate that intermediate ants ran faster at Bossou than they did at Taii. This suggests that a different

mechanism, such as social transmission, results in Taii chimpanzees using significantly shorter tools than Bossou chimpanzees when dipping for intermediate ants at nests. In the context of termite fishing at Gombe, tool insertion length of juvenile female chimpanzees was shown to correlate with their mother's indicating that some kind of social-learning process is involved in the acquisition of this task (Lonsdorf et al. 2004; Lonsdorf 2005). Similarly, young chimpanzees at Taii might learn to use relatively short tools either through direct observation of their mother or other models, or by using their mothers' tools as has been shown to occur in the acquisition of nut-cracking behaviour (Boesch 1991; Inoue-Nakamura & Matsuzawa 1997).

We did not find differences in availability that could account for Taii chimpanzees not dipping for intermediate species at trails. Instead another ecological difference, namely lower yield when dipping at trails at Taii, may be the cause. The small sample size of intermediate species did not, however, allow us to address this point in the current study.

We could not confirm any of our predictions of an ecological explanation for the lack of dipping for epigaeic species at Taii. Epigaeic ants were clearly more aggressive and persistent in defending their nests, which contain brood and the valuable queen, than foraging trails. However, we did not find any difference in defence behaviour (speed and persistence) of ants between sites. Owing to the small sample size, we might not have had enough statistical power to detect a site effect. However, the effect sizes we found suggest that, if an effect existed, it seems unlikely it would be of much biological relevance. Contrary to our prediction for an ecological explanation, yield at nests of epigaeic species

was higher at Taï than at Bossou; dipping for epigaeic ants at nests would therefore be at least as rewarding at Taï as it is at Bossou. Taï chimpanzees should be expected to dip unless they have easier access to brood than Bossou chimpanzees. Fat content assessed by petroleum ether extraction (Soxhlett) by Sylvia Ortmann (Institute of Zoo and Wildlife Research, Berlin, Germany) of separate samples of adult ants and the respective brood (eggs and larvae) of four different army ant species from Taï showed that brood contains about three times more fat than ants do (unpublished results). Manual extraction of brood by C. Schönig from three nests of each of the three epigaeic species at Taï resulted in up to 60 g of brood and ants per handful. This represents three times the weight from an average ant-dipping session at Gombe (McGrew 1974) and three times the weight from our dipping experiments at Taï (mean = 19.98 g, range 2.89–39.85 g, $N = 15$) and indicates that chimpanzees do gain more energy per unit time from a direct attack on brood than they do from dipping. However, access to brood did not differ between Bossou and Taï. Variation in the architecture of nest entrances therefore did not account for the observed differences in chimpanzee predation behaviour, and we are left to wonder why Bossou chimpanzees do not extract brood more often. Apart from the behaviour of the ants, other ecological factors might explain the difference in chimpanzee predation on epigaeic species. For example, Bossou chimpanzees eat very little meat (Sugiyama & Koman 1987; Hirata et al. 2001) and therefore may be in more need of animal protein and thus less selective in targeting army ants than Taï chimpanzees who hunt regularly (Boesch & Boesch 1989). However, Taï females consume substantially less meat than males (Boesch & Boesch-Achermann 2000) and dipping for epigaeic ants would therefore be beneficial to them, as chimpanzee females in general are more insectivorous whereas males consume more meat (McGrew 1979; Uehara 1986).

We hence suggest that cultural differences based on social learning remain the most parsimonious explanation for the observed differences in tool length when dipping for intermediate species at nests and for the variation in predation strategies on epigaeic species between the two chimpanzee populations. When dipping for fast-running ants, chimpanzees need to use longer tools to avoid getting bitten by ants running up the tool. Longer tools require a different technique to harvest ants from the tool, either the two-handed, pull-through technique or sideways sweep as used by Bossou chimpanzees. Why have chimpanzees at Taï not started using longer tools and invented the two-handed, pull-through technique or at least the sideways sweep? Social norms or conformity, as observed in the cultural differences in the use of leaf clipping, knuckle-knock or other communicative signals in chimpanzees, might explain this (Boesch 1996, 2003). Supporting this, an experimental study with captive chimpanzees on social transmission of a technique used to retrieve food from a box has shown that individuals who had accidentally invented a new technique did not pursue this one but

rather went back to using the socially dominant method originally introduced into their group (Whiten et al. 2005). The observation by Boesch & Boesch (1990) of one adolescent female briefly trying to dip for an epigaeic species shows that there is potential for innovation. However, similar to the captive study, conformity of the inventor to the behaviour of the community might prevent the spread of a new variant of an established behaviour.

Furthermore, independent of tool properties and associated technique, even prey consumption itself may be socially mediated. East African chimpanzees catch and eat not only arboreal monkeys, but also young bushpigs and duikers (Mahale, Tanzania, Nishida et al. 1979; Gombe, Goodall 1986; Ngogo, Uganda, Mitani & Watts 1999), whereas Taï chimpanzees have never been observed to catch bushpigs (Boesch & Boesch 1989) and they ignore duikers as prey even though they sometimes catch them and play with them (at Taï: Boesch & Boesch 1989; at Bossou: Sugiyama & Koman 1987; Hirata et al. 2001). Preference for certain parts of animal prey may also be culturally transmitted (Boesch & Boesch 1989). Similarly, young chimpanzees at Taï might not try to dip for epigaeic species because they do not observe their mothers do so. Neither do they spend much time at nests of epigaeic species, precluding the opportunity for individual learning. A study of social influences on the acquisition of ant dipping in Bossou chimpanzees has indeed shown that observation and learning opportunity are vital in the acquisition of ant dipping among young chimpanzees (T. Humle, C. T. Snowdon & T. Matsuzawa, unpublished data).

We thus suggest a complex interplay between ecological and cultural influences in army ant predation by wild chimpanzees. This is probably the case for the acquisition and maintenance of many behavioural traditions (Laland & Janik 2006). Natural selection favours adaptation to the environment an animal lives in but this process can be shaped by cultural factors leading to the use of different strategies or techniques. Assuming that in this study a genetic basis can be ruled out since both populations belong to the same subspecies, this in-depth comparison of prey behaviour and its ecology indicates the complexity of cultural processes. Cultural transmission might affect only some aspects of a general task, whereas others reflect rather a behavioural adaptation to environmental conditions. Future direct observations on the predation behaviour of chimpanzees at other sites where they have so far only indirectly been shown to prey on army ants will hopefully further expand our knowledge of this complex predator–prey interaction. Data on the ontogeny of ant dipping are difficult to obtain because, unlike termite fishing and nut cracking, it is a rare behaviour, but these data are urgently needed to help us understand the learning mechanisms that are involved in the acquisition of ant dipping. We hope that our study will encourage others investigating cultural transmission in wild animals to conduct similar detailed comparative work to test for ecological differences between populations facing similar ecological challenges.

Acknowledgments

We thank F. Djezia and the local assistants at Bossou for help in the field, R. Mundry for statistical advice, J. Riedel for participation in the interobserver reliability test, C. Schöning for checking army ant identifications and extracting brood from nests, and S. Ortmann for nutritional analysis of ant and brood samples from Tai. We are grateful to C. Schöning, R. Mundry, M. Robbins, M. Arandjelovic, C. Tennie and two anonymous referees for valuable comments on the manuscript. Y.M. and C.B. thank the Centre Suisse de Recherches Scientifiques at Abidjan for logistical support. All research at Tai and by Y.M. and C.B. was funded by the Max-Planck Society, while research at Bossou was funded by the Ministry of Education, Science, and Culture, Japan to T.M. and a NIH Kirschstein-NRSA Postdoctoral Fellowship to T.H.

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