Original Article

A case of mental time travel in ant-following birds?

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Army ant-following birds that inspect bivouacs (temporary nests of nomadic army ants) might provide a novel candidate for studying elements of mental time travel in animals, namely the ability to (1) remember the time and place of specific past events and (2) to use this memory to plan for future actions. Army ant colonies are a rich but unpredictable resource: Army ants do not raid every day, and colonies cycle through periods of high and low raid activity. Birds check bivouacs in the afternoon after feeding on insects that flee the army ant raids and then return to the bivouac the next morning to observe ant activity. If the ants are raiding, the birds will follow the army ants to the front of the raid and begin feeding; if not, the birds must move on to another army ant colony. Do ant-following birds check bivouacs to encode the location in their memory, thereby allowing them to return the next morning to feed again? Ant-following birds may track multiple army ant colonies through space and time to ensure a daily meal on an otherwise scattered and unpredictable resource. We suggest further research to test this hypothesis and provide a framework for investigating whether or not cognitive processes involved in mental time travel play a role in bivouac-checking behavior observed in the field. Key words: ant-following birds, bivouac checking, Eciton burchellii, learning, memory, mental time travel. [Behav Ecol]

WHAT IS MENTAL TIME TRAVEL?

The question of whether humans are unique among animals in their ability to travel mentally in time has been hotly debated (see Suddendorf and Corballis 2007 and associated commentaries). Mental time travel consists of 2 elements: the ability to remember past events (episodic memory) and the ability to anticipate and plan for future ones (future thinking). It is impossible to know whether nonhuman animals can recall past events and imagine possible future scenarios in the absence of any agreed behavioral markers of consciousness in nonlinguistic creatures nor whether they can recognize such memories and plans as their own, which is a fundamental feature of the phenomenology of human episodic memory (e.g., Tulving 2002). Clayton and her colleagues argued that it is possible to develop behavioral criteria, and in the absence of phenomenology, she termed the ability of animals to remember the where and when of past events “episodic-like memory” (Clayton and Dickinson 1998; Clayton et al. 2005). The advantage of this definition is that it makes episodic-like memory empirically tractable in both nonlinguistic animals and preverbal children (Clayton and Russell 2009). Similarly, Clayton et al. (2003) argued that one can test the behavioral components of future planning, namely whether animals can plan for a future event, taking action now for a future motivational state independent of their current needs. Testing the criteria for both retrospective and prospective cognition involves measuring 3 elements of an animal’s behavior: 1) An ability to update the content of a memory about what happened where and when, 2) Forming an integrated representation of a past event, and 3) Exhibiting flexibility in what response is made following the memory update (Clayton et al. 2003).

EVIDENCE FOR MENTAL TIME TRAVEL IN ANIMALS

A number of animals, including corvids (birds that are members of the crow family) and chickadees, rats and great apes, can remember past events in terms of what happened where and when and therefore possess episodic-like memory (e.g., Clayton and Dickinson 1998; Feeney et al. 2009; Zinkivskaya et al. 2009; Zhou and Crystal 2009; Martin-Ordas et al. 2010). There is also some evidence of future planning in primates and corvids (e.g., Correia et al. 2007; Raby et al. 2007; Osvath 2009). At issue, however, is whether animals engage in mental time travel. A skeptic would argue that animals just know about the past and future without traveling mentally in time to recall the past and imagine the future (e.g., Shettleworth 2010). Furthermore, because these abilities have been assayed in only a handful of taxa, it is unclear how often, and under what ecological conditions, episodic-like memory and future planning evolves.

We propose that bivouac checking, a specialized behavior of birds that interact with army ants, provides unique opportunities to expand our understanding of episodic-like memory in an evolutionarily relevant context. Diverse Neotropical army ant-following birds investigate army ant nest sites and provide a candidate system for the study of episodic-like memory and future planning in the wild. New evidence for taxonomically widespread performance of bivouac checking provides potential for identifying the ecological opportunities that favor episodic-like memory and future planning.
ANT-FOLLOWING BIRD BIVOUAC-CHECKING BEHAVIOR

Bivouac checking is a specialized behavior in which a bird follows *Eciton burchellii* army ants back to their temporary nest (called a bivouac) to inspect its location and assess ant foraging activity (Swartz 2001). Bivouac-checking birds visit *E. burchellii* colonies in the evening and then return the next morning to check the bivouac before feeding at the ants’ raid. When raiding, hundreds of thousands of *E. burchellii* workers swarm across the forest floor flushing leaf-litter dwelling arthropods (Schneirla 1971). A diverse guild of bird species attend army ant raids and forage on invertebrates fleeing from the ants (see Willson 2004). In tropical Neotropical forests, bivouac-checking behavior is performed almost exclusively by obligate ant-following birds (Brumfield et al. 2007) from a few families (Willis and Oniki 1978; Swartz 2001; Chaves-Campos 2003). In highland Neotropical forests, bivouac checking also occurs in facultative ant-following birds from diverse families (O’Donnell et al. 2010). Although ant-following birds forage at the raids of several species of army ant, bivouac checking has only been observed at *E. burchellii* bivouacs (Swartz 2001; O’Donnell et al. 2010).

Bivouac-checking behavior may require episodic-like memory. To understand why, it is necessary to first consider *E. burchellii* behavior. *Eciton burchellii* colonies have 2 activity phases: statary (or “stationary”) and nomadic. The statary phase occurs when the brood are in the egg and pupal stages, both of which are nonfeeding (Schneirla 1971). Colonies often skip raiding altogether on several days during the statary phase (Willis 1967; Schneirla 1971), making them temporally unreliable as a food resource for raid-attending birds. Statary colonies are spatially predictable because the ants keep the bivouac in the same location during this roughly 20-day period, raiding the surrounding forest in a radial pattern. Although the middle 2 weeks of the statary phase have few raids, the first and last few days of this phase see an increase of activity before entering the nomadic phase (Willis 1967). After the eggs develop into larvae and the pupae emerge as adults simultaneously, the approximately 14-day nomadic phase begins. The ants then raid through the forest on nearly all days to feed their hungry brood as well as themselves. During this stage, they move the bivouac to a new location (up to 150 m linear distance) almost every night and are thus able to cover new ground with fresh resources each morning. This makes the ants a spatially unreliable resource: Birds must track colony movements to locate raids on successive days.

Bivouac checking may allow birds to reduce uncertainty about whether a statary colony will raid and where a nomadic colony will raid. After feeding at a raid in the late afternoon, bivouac-checking birds follow the column of ants back to the bivouac and observe the location of the mass of ants (which is sometimes hidden inside a shelter, such as a tree trunk; Swartz 2001; O’Donnell S, personal observation). If the ants are emigrating to a new bivouac site, the birds will follow the ant column. If the ants do not move, the birds return to the bivouac the next morning and, if the ants have begun raiding again, follow the column of ants to the front of the new raid and forage as they did the day before (Swartz 2001; Chaves-Campos 2003). If the bivouac was moved after dark, the birds will follow the raid path created the previous day and search for the ants’ new bivouac or raid location (Swartz 2001). That *E. burchellii* use the previous day’s raid path to reposition their bivouac (see Willson 2004) means that following this path is likely to lead to their new location.

Colonies of *E. burchellii* in the statary phase may not raid every day; therefore, obligate ant-following birds must track and remember several colonies at one time. When *E. burchellii* colonies coincide geographically, they are not in developmental synchrony (Schneirla 1971). Therefore, although many colonies can exist in one area, their phases are independent from one another (i.e., some colonies may be at varying stages of the statary phase, whereas others may be at varying stages of the nomadic phase). Willson (2004) estimates that birds tracking at least 3 *E. burchellii* colonies will have a high probability of encountering a raid daily.

A CASE FOR EPISODIC-LIKE MEMORY IN ARMY ANT-FOLLOWING BIRDS?

We propose that the bivouac-checking behavior of *E. burchellii*-following birds is a candidate for episodic-like memory. Episodic-like memory is indicated through bivouac inspection: The birds appear to encode at least the ants’ location (where) in order to return the next morning. These birds may exhibit episodic-like memory by returning to the right bivouacs at the correct location and at the appropriate time. In determining which bivouac is the “right bivouac” to check, birds should preferentially check those bivouacs from *E. burchellii* colonies in the nomadic phase (the closer to the beginning of this phase the better) or near the end of the statary phase when raid activity begins to increase (“the correct time”) because there is a higher pay off in terms of likelihood of raiding on a given day (Willis 1967; Willson 2004). The “correct location” is needed to remember where the nomadic bivouacs are located. The correct time could also mean that they check the bivouac before the ants start raiding, which gives the birds the opportunity to be the first to arrive at the raid (Chaves-Campos 2003). Consequently, bivouac-checking birds may update the content of their memory as the army ants change phase and location, which may require elements of the memory of what (colony), when (nomadic or statary phase), and where (bivouac location) to be integrated into one event which may be used flexibly if the birds check nomadic or late-stage statary bivouacs first or more often.

Tracking bivouacs mentally in time may confer certain advantages to birds carrying out this behavior. Bivouac-checking birds are often primarily insectivores, and insects are a patchy resource. An army ant raid provides an abundant source of prey; however, raids are widely and unpredictably spaced (about 5 colonies per 100 ha; Willson 2004) and much time and energy can be wasted searching for a raid to attend. It is therefore not surprising that some *E. burchellii*-following birds, the bivouac checkers, possess the ability to keep track of the army ants. We hypothesize that bivouac-checking birds may remember, which *E. burchellii* colonies (what) are in which locations (where) and what phase (statary or nomadic) the colony is in (when) and that they may be using episodic-like memory if they prefer to check those bivouacs from army ant colonies in the nomadic phase.

Field data indicate that bivouac-checking birds remember bivouac locations (where). Now the question is whether they remember which ant colony (what, where) is in the nomadic phase (when).

EMPIRICAL TESTS OF EPISODIC-LIKE MEMORY IN BIVOUAC-CHECKING BIRDS

We hope to inspire investigations of episodic-like memory in bivouac-checking birds and offer a framework for doing so, highlighting the importance of conducting ecologically relevant studies specific to each species and their unique life history (e.g., Real 1993; Kamil 1994; Clayton et al. 2001; Emery and Clayton 2004). We suggest further field research on bivouac-checking behavior to confirm a few key details
necessary for qualification as a candidate for episodic-like memory. If field research appears to support the hypothesis that bivouac-checking birds have episodic-like memory, then we suggest carrying out controlled experiments in the laboratory to investigate the behavioral criteria of episodic-like memory, including the content, structure, and flexibility of the memory.

Field studies

If bivouac-checking birds prefer to check *E. burchelli* bivouacs that are in the nomadic phase, then this indicates that they may be keeping track of which *E. burchelli* colonies (what) have bivouacs in which locations (where) and what phase they are in (when). To explore this hypothesis, field data should be collected to answer the following questions:

1. How many bivouacs are tracked at once and for how long?
   - If multiple bivouacs are tracked at one time, then birds will need to remember where each bivouac is located. If birds exclusively, or first and more frequently, check those bivouacs of *E. burchelli* in the 14-day resource-abundant nomadic phase and then refrain from checking stationary bivouacs until the last week of this phase (when), then they may be using episodic-like memory to process this information. The variation in food abundance produced in the 2 *E. burchelli* phases indicates that there is a correct type of bivouac to check to maximize the time and energy spent tracking *E. burchelli* versus the food rewards gained. Ocellated antbirds check between 1 and 5 *E. burchelli* colonies per day (Chaves-Campos 2011), demonstrating that at least one species possesses the tracking capability necessary to perform this behavior. It is possible that the birds attend to external cues to find raids rather than solely on memory. Three such cues include: increased activity near the end of the stationary phase which could be used to predict the start of the nomadic phase, the presence of cocoon shells near the bivouac which appear just before the ants enter the nomadic phase, and social facilitation of bird movement from one raid to another (Chaves-Campos 2011; Chaves-Campos J. personal communication). The relative importance of external cues and memory will need to be determined when examining this behavior.

2. How do birds find bivouacs that were moved during the night?
   - a. Are bivouacs checked at dusk to follow the *E. burchelli* emigration and determine the location of the new bivouac site? If this occurs, then the bird must remember location information from the evening bivouac check in order to find that bivouac again the next morning when the ants start raiding again. Sometimes bivouac emigration occurs after dark (O’Donnell et al. 2010) at which point the bird would need to use the strategy of following the raid path from the previous day to find the next morning’s bivouac location since this is where army ants relocate their bivouacs (see Wilson 2004) or follow other birds from the old to the new bivouac location (Chaves-Campos 2011).
   - b. Do birds roost in the vicinity of the bivouac? If so, they do not need to rely on extensive memory to relocate the bivouac. There is evidence that, at least for Ocellated and Bicolored Antbirds, roosting areas are small and territorial compared with feeding ranges which are large and overlap with neighboring birds (Willis 1967; Chaves-Campos and DeWoody 2008), indicating that birds do not roost in the vicinity of the bivouac and therefore probably rely on memory to relocate it. Further study on this species revealed that bivouacs nearer the roosting sites are checked first and then others are checked depending on the raiding activity of the first colony (Chaves-Campos 2011). Additionally, prey intake rates are maximized due to increased dominance rank when attending raids within an individual’s roosting area (Willis 1967; Chaves-Campos et al. 2009). Thus, it appears that although the convenient and more productive bivouacs are checked first, the birds still possess the ability to track more distant colonies and encounter them as needed.

Confirming episodic-like memory through controlled experiments

If field studies demonstrate that bivouac-checking birds may remember which bivouac was checked and what phase the associated *E. burchelli* colony was in, the next step would be to experimentally explore the cognitive mechanisms that allow them to do so. Examining episodic-like memory requires the experimenter to vary which army ant colonies (what) are in which bivouac locations (where), and the timing of colonies in early stationary versus late stationary and nomadic phases (when). It will also be important to determine if birds are solving the bivouac-checking task through automatic behavior (cues from olfaction, vision, or circadian rhythm; see Clayton and Dickinson 1998 for a case study).

A CASE OF FUTURE PLANNING IN ARMY ANT-FOLLOWING BIVOUAC-CHECKING BIRDS?

We suspect that future planning could be involved in bivouac-checking bird behavior because birds check bivouacs when sated (conferring no immediate benefit), a behavior that does not make sense until the next morning on return to the bivouac when the bird finds the ants raiding again and encounters its next meal (a delayed benefit). Because bivouac checking occurs after foraging at a raid, there is no immediate benefit to conducting this behavior in terms of acquiring a meal in the next few minutes. Instead, the benefit occurs the next morning when the ants begin raiding again; bivouac-checking birds return and are the first to begin foraging at the raid (Swartz 2001; Chaves-Campos 2003). This could indicate a dissociation between their current state (sated) and a future need (will need to eat tomorrow), which suggests anticipation of future events (Clayton et al. 2003).

It is important to determine if bivouac-checking birds meet the behavioral criteria for future planning (Clayton et al. 2003). If they do, the additional element of a delayed payoff (check now to forage later) further strengthens their case as a candidate for future planning. One could test whether bivouac-checking birds choose to check bivouacs only in the morning (indicating their interest in the immediate payoff of an active *E. burchelli* raid) or if they also check bivouacs in the evenings and if the latter occurs, examine if the function is to determine the location of the new bivouac in anticipation of breakfast the next morning. Many bivouac-checking bird species visit bivouacs in the morning and at night (O’Donnell et al. 2010; Chaves-Campos 2011), confirming that the birds possess this capability. Further investigation in the laboratory to determine which mechanisms are used to conduct this behavior will be crucial.

WHAT MAKES BIVOUAC-CHECKING BIRDS DIFFERENT?

Of the hundreds of species of birds that follow *E. burchelli* raids, only 21 are known to check bivouacs (Table 1; Swartz 2001; Chaves-Campos 2003; O’Donnell et al. 2010). *Ecton*
There is evidence of episodic-like memory and future planning in some nonhuman animals. Here, we argue that the behavior of army ant-following bivouac-checking birds is an interesting candidate for studying episodic-like memory and future planning in the wild and suggest further studies to evaluate this claim. The most convincing evidence for mental time travel comes from apes and corvids, yet it remains to be tested whether mental time travel is restricted to these taxa. If we learn episodic-like memory is more widespread, we are encouraged to look for patterns of ecological challenges that are associated with its performance in diverse taxa.

Regardless of what future investigations learn about the presence or absence of mental time travel in bivouac-checking birds, this behavior is interesting for other ecological and psychological reasons. This system is an excellent model for further investigations of tracking behavior, avian dependence on army ants, and temporal discounting (do bivouac checkers choose to check stationary bivouacs nearby [low energetic cost and low food reward] or will they travel farther away to check bivouacs in the nomadic phase [higher energetic cost and higher food reward]) to name a few.

**REFERENCES**


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