

Forum: Ideas

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

Corina J. Logan,<sup>a</sup> Sean O'Donnell,<sup>b</sup> and Nicola S. Clayton<sup>a</sup>

<sup>a</sup>Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK and

<sup>b</sup>Animal Behavior Program, Department of Psychology, University of Washington, Seattle, WA 98195, USA

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* 22:1149–1153 (2011)]

## 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. 2003). 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 animals' 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; Zinkivskay 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.

Address correspondence to C.J. Logan. E-mail: c1417@cam.ac.uk.

Received 3 November 2010; revised 30 April 2011; accepted 24 May 2011.

## 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 lowland 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: statory (or "stationary") and nomadic. The statory 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 statory phase (Willis 1967; Schneirla 1971), making them temporally unreliable as a food resource for raid-attending birds. Statory 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 statory 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 statory 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 statory 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 statory 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 statory 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 statory phase), and where (bivouac location) to be integrated into one event which may be used flexibly if the birds check nomadic or late-stage statory 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 (statory 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. burchellii* bivouacs that are in the nomadic phase, then this indicates that they may be keeping track of which *E. burchellii* 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. burchellii* in the 14-day resource-abundant nomadic phase and then refrain from checking stately 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. burchellii* phases indicates that there is a correct type of bivouac to check to maximize the time and energy spent tracking *E. burchellii* versus the food rewards gained. Ocellated antbirds check between 1 and 5 *E. burchellii* 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 stately 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. burchellii* 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 Willson 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. burchellii* 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 stately versus late stately 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 BIVOAC-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. burchellii* 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 BIVOAC-CHECKING BIRDS DIFFERENT?

Of the hundreds of species of birds that follow *E. burchellii* raids, only 21 are known to check bivouacs (Table 1; Swartz 2001; Chaves-Campos 2003; O'Donnell et al. 2010). *Eciton*

Table 1

Twenty-one bird species from 13 families are known to check bivouacs; all are altricial (part of their developmental period is spent with their parents; Gill 1995; Garrigues and Dean 2007)

Common name	Scientific name	Family	Family distribution	Present at elevation (m)	Present at study sites <sup>a</sup>
Obligate ant-followers					
Gray-headed tanager <sup>1</sup>	<i>Eucometis penicillata</i>	Thraupidae	Neotropics	0–1350	1, 3
Bicolored antbird <sup>1,2</sup>	<i>Gymnopithys leucaspis</i>	Thamnophilidae	Neotropics	0–1200	1, 2
Tawny-winged woodcreeper <sup>1</sup>	<i>Dendrocincla anabatina</i>	Dendrocolaptidae	Neotropics	0–1500	1
Ocellated antbird <sup>2</sup>	<i>Phaenostictus mcleannani</i>	Thamnophilidae	Neotropics	0–1200	2
Spotted antbird <sup>2</sup>	<i>Hylophylax naevioides</i>	Thamnophilidae	Neotropics	0–1000	2
Plain-brown woodcreeper <sup>2</sup>	<i>D. fuliginosa</i>	Dendrocolaptidae	Neotropics	0–900	2
Ruddy woodcreeper <sup>3</sup>	<i>D. homochroa</i>	Furnariidae	Neotropics	500–1350	1, 3
Facultative ant-followers					
Northern barred woodcreeper <sup>1,2</sup>	<i>Dendrocolaptes sanctithomae</i>	Dendrocolaptidae	Neotropics	0–1300	1, 2, 3
Black-cheeked ant-tanager <sup>1</sup>	<i>Habia atrimaxillaris</i>	Thraupidae	Neotropics	0–~100	1
Cocoa woodcreeper <sup>1</sup>	<i>Xiphorhynchus susurrans</i>	Dendrocolaptidae	Neotropics	0–900	1, 2
White-whiskered puffbird <sup>1</sup>	<i>Malacoptila panamensis</i>	Bucconidae	Neotropics	0–1000	1, 2
Orange-billed nightingale thrush <sup>3</sup>	<i>Catharus aurantiirostris</i>	Turdidae	Worldwide	500–2200	3
Chiriqui quail dove <sup>3</sup>	<i>Geotrygon chiriquensis</i>	Columbidae	Worldwide	600–2400	2, 3
Blue-crowned motmot <sup>3</sup>	<i>Momotus momota</i>	Momotidae	Neotropics	0–2000	1, 2, 3
White-eared ground sparrow <sup>3</sup>	<i>Melospiza leucotis</i>	Emberizidae	Neotropics	1000–2000	3
Rufous-capped warbler <sup>3</sup>	<i>Basileuterus rufifrons</i>	Parulidae	New World	0–2000	2, 3
Rufous-and-white wren <sup>3</sup>	<i>Thryothorus rufalbus</i>	Troglodytidae	Neotropics	0–1100	3
Emerald toucanet	<i>Aulacorhynchus prasinus</i>	Rhamphastidae	Neotropics	800–2400	2, 3
Chestnut-capped brush finch	<i>Buarremon brunneinucha</i>	Emberizidae	Neotropics	900–2500	2, 3
White-breasted wood wren	<i>Henicorhina leucosticta</i>	Troglodytidae	Neotropics	0–1800	1, 3
Slaty-backed nightingale thrush	<i>C. fuscater</i>	Turdidae	Worldwide	800–1800	2, 3

<sup>a</sup> Costa Rica study site numbers: 1 = Osa Peninsula (Swartz 2001), 2 = Puerto Viejo de Sarapiquí (Chaves-Campos 2003), 3 = Monteverde (O'Donnell et al. 2010; O'Donnell S, personal observation).

*burchellii* phase schedules (nomadic vs. stately) remain relatively constant; however, the bird species that perform bivouac-checking behavior vary by geographic location (O'Donnell et al. 2010). Given the specificity of bivouac checking and the possibility that this behavior could indicate certain cognitive abilities, namely episodic-like memory and planning for the future, one would expect to find certain life-history differences in those species able to track army ants compared with those who do not. Longevity, long-developmental periods, and sociality have been implicated as factors involved in complex cognition and may play a role in the learning or performance of bivouac-checking behavior (Humphrey 1976; Brawn et al. 1995; Swartz 2001; Emery et al. 2007). However, there is a paucity of natural history data on many species of Neotropical birds; thus, confirmation of these conjectures is dependent on further research.

It is unknown whether bivouac-checking behavior exists in Old World army ant-following birds as this system has a scarcity of data compared with New World *E. burchellii*-following birds (Peters et al. 2008). Documenting the presence or absence of bivouac-checking behavior in Old World army ant-following birds would be an important comparison for New World birds in order to understand the evolution of this behavior and determine if it is more prevalent in particular habitats.

## CONCLUSION

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 stately 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.

## FUNDING

Gates Cambridge Trust and Murray Edwards College Overseas Bursary to C.J.L.; National Science Foundation (IBN-0347315 and IOS-0923680), University of Washington Royalty Research Fund, and National Geographic Television to S.O'D.; and grants from University of Cambridge, Clare college and Leverhulme Trust to N.S.C.

We thank Lucy Cheke, Ljerka Ostojic, and James Thom for helpful feedback; and Dr Johel Chaves-Campos, Dr Lucie Salwiczek, Dr Uri Grodzinski, and Dr Caroline Raby for discussions and comments on an earlier draft of this manuscript.

## REFERENCES

- Brawn JD, Karr KR, Nichols JD. 1995. Demography of birds in a neotropical forest: effects of allometry, taxonomy, and ecology. *Ecology*. 76:41–51.
- Brumfield RT, Tello JG, Cheviron ZA, Carling MD, Crochet N, Rosenberg KV. 2007. Phylogenetic conservatism and antiquity of a tropical

- specialization: army-ant-following in the typical antbirds (Thamnophtidae). *Mol Phylogenet Evol.* 45:1–13.
- Chaves-Campos J. 2003. Localization of army-ant swarms by ant-following birds on the Caribbean slope of Costa Rica: following the vocalization of antbirds to find the swarms. *Ornitol Neotrop.* 14:289–294.
- Chaves-Campos J. 2011. Ant colony tracking in the obligate army ant-following antbird *Phaenostictus mcleannani*. *J Ornithol.* 152: 497–504.
- Chaves-Campos J, Araya-Ajoy Y, Lizana-Moreno CA, Rabenold KN. 2009. The effect of local dominance and reciprocal tolerance on feeding aggregations of ocellated antbirds. *Proc R Soc B Biol Sci.* 276:3995–4001.
- Chaves-Campos J, DeWoody A. 2008. The spatial distribution of avian relatives: do obligate army-ant-following birds roost and feed near family members? *Mol Ecol.* 17:2963–2974.
- Clayton NS, Bussey TJ, Dickinson A. 2003. Can animals recall the past and plan for the future? *Nat Rev Neurosci.* 4:685–691.
- Clayton NS, Dickinson A. 1998. Episodic-like memory during cache recovery by scrub-jays. *Nature.* 395:272–278.
- Clayton NS, Griffiths DP, Emery NJ, Dickinson A. 2001. Elements of episodic-like memory in animals. *Philos Trans R Soc Lond B Biol Sci.* 356:1483–1491.
- Clayton NS, Russell J. 2009. Looking for episodic cognition in animals and young children: prospects for a new minimalism. *Neuropsychologia.* 47:2330–2340.
- Correia SPC, Dickinson A, Clayton NS. 2007. Western scrub-jays (*Aphelocoma californica*) anticipate future needs independently of their current motivational state. *Curr Biol.* 17:856–861.
- Emery NJ, Clayton NS. 2004. The mentality of crows. Convergent evolution of intelligence in corvids and apes. *Science.* 306:1903–1907.
- Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007. Cognitive adaptations of social bonding in birds. *Philos Trans R Soc Lond B Biol Sci.* 362:489–505.
- Feeney MC, Roberts WA, Sherry DA. 2009. Memory for what, where, and when in the black-capped chickadee (*Poecile atricapillus*). *Anim Cogn.* 12:767–777.
- Garrigues R, Dean R. 2007. *The birds of Costa Rica.* Ithaca (NY): Zona Tropical.
- Gill FB. 1995. *Ornithology.* New York: W. H. Freeman.
- Humphrey NK. 1976. The social functions of intellect. In: Bateson PPG, Hinde RA, editors. *Growing points in ethology.* Cambridge: Cambridge University Press. p. 303–317.
- Kamil AC. 1994. A synthetic approach to the study of animal intelligence. In: Real L, editor. *Behavioral mechanisms in evolutionary ecology.* 2nd ed. Chicago (IL): University of Chicago Press. p. 11–45.
- Martin-Ordas G, Haun D, Colmenares F, Call J. 2010. Keeping track of time: evidence for episodic-like memory in great apes. *Anim Cogn.* 13:331–340.
- O'Donnell S, Kumar A, Logan C. 2010. Species differences in army ant raid attendance and bivouac checking behavior among Neotropical montane forest birds. *Wilson J Ornithol.* 122:503–512.
- Osvath M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Curr Biol.* 19:R190–R191.
- Peters MK, Likare S, Kraemer M. 2008. Effects of habitat fragmentation and degradation on flocks of African ant-following birds. *Ecol Appl.* 18:847–858.
- Raby CR, Alexis DM, Dickinson A, Clayton NS. 2007. Planning for the future by Western scrub-jays. *Nature.* 445:919–921.
- Real LA. 1993. Toward a cognitive ecology. *Trends Ecol Evol.* 8: 413–417.
- Schneirla TC. 1971. *Army ants: a study in social organization.* San Francisco (CA): W. H. Freeman.
- Shettleworth SJ. 2010. *Cognition, evolution, and behavior.* 2nd ed. Oxford: Oxford University Press.
- Suddendorf T, Corballis MC. 2007. The evolution of foresight: what is mental time travel and is it unique to humans? *Behav Brain Sci.* 30:299–313.
- Swartz MB. 2001. Bivouac checking, a novel behavior distinguishing obligate from opportunistic species of army-ant-following birds. *Condor.* 103:629–633.
- Tulving E. 2002. Episodic memory: from mind to brain. *Annu Rev Psychol.* 53:1–25.
- Willis EO. 1967. The behavior of bicolored antbirds. *Univ Calif Publ Zool.* 79:1–132.
- Willis EO, Oniki Y. 1978. Birds and army ants. *Annu Rev Ecol Syst.* 9:243–263.
- Willson SK. 2004. Obligat army-ant-following birds: a study of ecology, spatial movement patterns, and behavior in Amazonian Peru. *Ornithol Monogr.* 55:1–67.
- Zhou W, Crystal J. 2009. Evidence for remembering when events occurred in a rodent model of episodic memory. *Proc Natl Acad Sci U S A.* 106:9525–9529.
- Zinkivskay A, Nazir F, Smulders TV. 2009. What-where-when memory in magpies (*Pica pica*). *Anim Cogn.* 12:119–125.