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Testing for sentinel coordination in Smooth-billed Anis (*Crotophaga ani*)

Jing Sheng Hing[1] · Gregory Schmaltz[2] · James S. Quinn[1]

Abstract

Sentinel behaviour has been widely described, but whether or not it is coordinated among group members requires careful examination. The Smooth-billed Ani, *Crotophaga ani*, a joint-nesting cooperatively breeding bird, appears to have a sentinel system; however, it is unknown whether that vigilance is coordinated, the defining feature of sentinel behaviour. We followed social groups during two breeding seasons to observe and time their individual sentinel bouts. We then tested for coordination by quantifying the observed and expected proportions of time during which (1) no sentinel was present during observations, and (2) two or more sentinels were present. The majority of social groups spent less time than expected, under the coordination hypothesis, with at least one sentinel, indicating evidence against coordinated vigilance. This was significant for social groups observed in 2015, but not in 2002. Across both years, temporal overlap in sentinel behaviour between two individuals occurred significantly less than expected under the coordination hypothesis. This study contributes to a gap in our knowledge of sentinel behaviour and suggests that Smooth-billed Anis lack organized vigilance, possibly due to low within-group relatedness and group instability.

Keywords Sentinel behaviour · Vigilance coordination · Cuckoo · Cooperative breeding · Coordination hypothesis

Zusammenfassung

Gibt es eine Wachtpostenkoordination bei Glattschnabelanis (*Crotophaga ani*)?

Wächterverhalten wurde bereits vielfach beschrieben, ob es jedoch auch zwischen den Mitgliedern einer Gruppe koordiniert wird, bedarf sorgfältiger Prüfung. Der Glattschnabelani (*Crotophaga ani*), ein sozialer, gemeinschaftlich nistender Vogel mit kooperativem Brutverhalten, scheint ein Wachtpostensystem zu besitzen. Es ist jedoch nicht bekannt, ob das Wachverhalten auch koordiniert wird, was ein Definitionskriterium für ein echtes Wachtpostenverhalten wäre. Über zwei Brutzeiten hinweg verfolgten wir die sozialen Gruppen, um deren individuelle Wächterphasen zu beobachten und jeweils deren Dauer zu messen. Anschließend testeten wir auf eine Koordination des Verhaltens, indem wir die beobachteten beziehungsweise erwarteten Zeitanteile verglichen, zu denen a) kein Wachtposten zum Beobachtungszeitpunkt anwesend war oder b) zwei oder mehr Wachtposten zugegen waren. Die Mehrzahl der sozialen Gruppen verbrachte weniger Zeit als zufällig zu erwarten mit mindestens einem Wachtposten, was gegen eine Koordination des Wachverhaltens spräche. Für die im Jahr 2015 beobachteten Gruppen war dies signifikant, für die in 2002 allerdings nicht. Diese Untersuchung liefert einen Beitrag zur Schließung der Wissenslücke über das Wachtpostenverhalten und deutet darauf hin, dass es bei Glattschnabelanis kein organisiertes Wächtersystem gibt, möglicherweise aufgrund niedriger Verwandtschaftsgrade innerhalb der Gruppen und von Gruppeninstabilität.

Introduction

Descriptive studies of several species report sentinel behaviour (reviewed in Bednekoff 2015). Up until now, most of these descriptive studies have focused on the presence or absence of sentinel behaviour. However, there is a dearth of studies that have quantitatively tested for coordinated

sentinel behaviour. Coordinated sentinel behaviour is defined as coordinated vigilance of sentinel bouts that are spread across time more evenly than expected by chance to reduce the amount of time when no sentinel is present (McGowan and Woolfenden 1989; Bednekoff 1997, 2015). Empirical evidence of a coordinated sentinel system in birds has only been reported in Florida Scrub Jays *Aphelocoma coerulescens* (McGowan and Woolfenden 1989; Bednekoff 2015), highlighting a large gap in our knowledge of this intriguing behaviour.

The use of sentinels in many social species is known to function as an anti-predator adaptation that confers a variety of benefits. Sentinel species can decrease per capita time spent scanning for predators, allowing for more dedicated time spent foraging, and earlier detection and avoidance of predators (McGowan and Woolfenden 1989; Manser 1999; Hollen et al. 2008; Ridley et al. 2010; Sorato et al. 2012). These advantages may be amplified by a coordinated system.

The cost of being a sentinel and the trade-off between foraging and the risk of predation are also likely to influence the evolution and maintenance of coordinated sentinel systems. For example, sentinel activity is known to correlate with satiation and energetic state. Although sentinels have the advantage of early detection of predatory threats, there is a cost in foraging opportunities such that the benefits of foraging increase the longer an individual is a sentinel. Studies have shown that individuals are more likely to be sentinels and remain so for longer periods of time when satiated (Bednekoff 2003) and when in possession of greater energy reserves (Wright et al. 2001a). It is also worth noting that sentinels are not necessarily safer than their foraging conspecifics, as one study showed that sentinels are further from cover than foragers and are more likely to be targeted by predators (Ridley et al. 2013). Therefore, a coordinated sentinel system whereby individuals coordinate sentinel bouts might allow individuals to share costs and benefits (Wickler 1985).

Apparent sentinel behaviour and coordinated sentinel behaviour have been observed in cooperative breeders across mammalian (Clutton-Brock et al. 1999; Rasa 1986) and avian (McGowan and Woolfenden 1989; Yasukawa and Cockburn 2009; Sorato et al. 2012; Ridley et al. 2013) taxa. Cooperative breeding brings individuals together in a situation whereby kin selection and/or reciprocity may set the stage for organized vigilance (McGowan and Woolfenden 1989). One reason why cooperative breeding may favour selection for coordinated sentinel behaviour relates to the potential fitness benefits sentinels may accrue (Bednekoff 1997, 2015). For example, in providing protection of adult genetic offspring in kin groups, individuals may obtain delayed benefits such as alloparental care and increased reproductive success (Komdeur

1995; Ekman et al. 2004). Kin selection may also lead to the formation of small and stable groups that favour coordinated vigilance as the time cost involved in monitoring group members is reduced (Bednekoff 1997; Ward 1985).

Smooth-billed Anis (*Crotophaga ani*) have been observed to use a functional referential alarm call system (FRAC) (Grieves et al. 2014), a trait that would support a coordinated sentinel system (Bednekoff 1997, 2015). An apparent sentinel system in Smooth-billed Anis was first described by Loflin (1983); however, whether or not the system is coordinated has not yet been examined. Smooth-billed Anis are joint-nesting cooperatively breeding Neotropical birds that form social groups ranging from two to 17 individuals, composed mostly of socially monogamous pairs (Quinn and Startek-Foote 2000). In these social groups, members share a joint nest, defend an all-purpose territory and forage together during the breeding season.

Smooth-billed Anis predominantly forage in open fields with occasional trees or snags (Quinn and Startek-Foote 2000). In this microhabitat, Smooth-billed Anis mostly forage on the ground for insects in short to medium grass (Quinn and Startek-Foote 2000). Smooth-billed Anis will search through the grass pouncing on insects and picking up insects stirred by movement (Quinn and Startek-Foote 2000; Davis 1940). While feeding on the ground, Smooth-billed Anis can be susceptible to predation, with visibility obstructed by grass. Indeed, species demonstrating coordinated and apparent sentinel systems often forage near the ground, where they are susceptible to predation and have limited predator-detection abilities (Gaston 1977; McGowan and Woolfenden 1989; Wright et al. 2001a). As such, Smooth-billed Ani sentinels foraging in open areas may use trees and snags as perches (Quinn and Startek-Foote 2000). Furthermore, with the advantages of foraging in social groups and FRAC, individuals may detect predation risks easier when acting as a sentinel. If energy thresholds and foraging abilities differ among group members, it would be optimal for individuals to perform sentinel duty when energy reserves are sufficient and no other bird is a sentinel (Bednekoff 1997).

We tested the hypothesis that Smooth-billed Anis have a coordinated sentinel system. This hypothesis predicts that sentinel bouts across time are spread out more evenly than expected by chance. Specifically, we predicted the observed proportion of time without a sentinel would not exceed the calculated expected (optimal) proportion of time without a sentinel. In addition, we predicted the observed proportion of time with overlaps between individuals would not exceed the expected proportion (optimal) of time where more than one individual would act as sentinels simultaneously (prediction 2).

Methods

Field site

Smooth-billed Anis were studied at the Cabo Rojo National Wildlife Refuge (CRNWR) in southwestern Puerto Rico (17°59″N, 67°10″W) from September to December 2002 and 2015. The CRNWR has a dry tropical climate with a pronounced rainy season typically from September to December and a dry season from January to April. A short increase in rain typically occurs in May, followed by dry conditions until September. CRNWR can be described as a subtropical, dry, scrubland in secondary succession with large open areas (Schmaltz et al. 2008). Here, Smooth-billed Anis typically breed during the rainy season and are resident year-round. They do not consistently hold territories during the dry season, roaming larger areas in loose, large foraging flocks (Quinn and Startek-Foote 2000).

Sentinel observations

We selected groups for observation based on how effectively group members could be distinguished. Banding efforts at CRNWR have been ongoing since 1998 and banded individuals are distinguishable by a unique combination of one metal band and three colour bands. To test for coordination in sentinel behaviour we chose groups where there were no more than two unbanded individuals. In each sentinel observation of groups that contained two unbanded individuals ($n = 5$), we were able to distinguish between the two individuals for the duration of the observation by tracking spatial location and movements of each unbanded individual relative to one another.

Each social group was followed over the following periods: 6–29 December 2002 and 7 October–14 December 2015. Sentinel observation bouts were conducted for 1–2 h periods using a Swarovski scope (ATX 25–60 x 65) and binoculars (Vortex Crossfire, 8×42) for 2015 and binoculars (Pentax, 8×42 and 10×42) for 2002. The use of a telescope and binoculars allowed us to maintain a fair distance (100–200 m) so that we did not affect the behaviour of the subjects. Observations in which the social group was lost from view before 1 h had elapsed were excluded from the analysis. In 2002, a total of five groups were followed and a total of 15 h of foraging observations were collected. Numbers of individuals in each group for 2002 were as follows: Gully (five), North Hillside (three), North East (five), US Flag (five), and Home (six). In 2015, a total of five groups were followed during the breeding season of 2015 and a total of 20 h of group foraging observations

were successfully collected. Numbers of individuals in each group for 2015 were: Gully (four), NFence (four), 4-way (five), EastT (three), Finka (five). All sentinel observations were conducted from 0800 to 1100 hours or 1530–1800 hours.

Individuals were classified as sentinels if they met the following criteria: (1) perched at least 1 m off the ground for at least 30 s in a conspicuous location near foragers, and (2) scanning the surrounding area. A stopwatch was used to keep track of observation times. The observation period began when the stopwatch started and lasted for 1–2 h. The observer would record the identity of the individuals acting as sentinels for the duration of the observation, taking note of the start and stop times of sentinel bouts to the nearest second.

Statistical analyses

All analyses were conducted in R version 3.1.2. (R Development Core Team 2014). First, we calculated the total amount of time spent as a sentinel for each individual and the total amount of time without sentinels during each observation. To calculate the expected proportion of time without a sentinel for each observation, the following formula was used:

$$\prod_{i=1}^{n}(1 - p_i)$$

where p_i is the proportion of time spent by an individual, i, on sentinel duty (Bednekoff 2015). This value was then compared to the observed proportion of time without a sentinel during that observation. We calculated the average observed and expected time without sentinels across sessions for each social group. Coordination was then measured as the difference between the average observed and expected time without a sentinel per group.

We also looked at the observed and expected proportions of overlap between all combinations of $n = 2$–5 birds (i.e. overlap between pairs, triplets etc.) for each observation session. To calculate the expected proportion of overlap for each combination of birds, we first multiplied the proportion of time each individual was a sentinel. We then multiplied that value by the proportion of time the remaining group members were not sentinels. So, for example, in a group of three birds (a, b, c), to calculate the expected proportion of overlap time between a and b:

$$(p_a \times p_b) \times (1 - p_c)$$

where p is the proportion of time spent by an individual on sentinel duty. We calculated the average observed and expected proportions of overlap time for every combination of $n = 2$–5 birds across observation sessions for each group to test for differences between observed and expected values.

To assess the difference between observed and expected proportion of time with no sentinel across both years we used a linear mixed effects model (LMM) using the nlme package (Pinheiro et al. 2016). In this model, the average proportion of time without a sentinel was the response variable. Year, Type (coded as a binary variable, i.e. observed or expected), and the interaction between these two variables were included as fixed effects. Social group was included as a random intercept in this model to account for statistical non-independence of our observations for each group. This LMM corresponds to a pooled *t*-test on Type.

To assess the overall difference between observed and expected proportions of overlap time, we conducted separate LMM for overlap between $n = 2$–5 birds. For each model, the response variable was the average proportion of time with overlap. Year, Type and the interaction between these two variables were included as fixed effects. Social group was included as a random intercept for each model. These LMM are also similar to conducting a pooled *t*-test on Type.

Results

Overall, across both years, there was a significantly greater proportion of the average observed time with no sentinel than expected [estimate = 0.0642, 95% confidence interval (CI) = (0.00739, 0.121), $df = 8$, $P = 0.0313$] (Fig. 1). Looking at the difference between the average observed and expected proportions of time with no sentinel in each year, there was a greater proportion of time observed than expected with no sentinel in 2002; however, this was non-significant [estimate = 0.0182, 95% CI = (− 0.0621, 0.0985), $df = 8$, $P = 0.615$] (Fig. 1). In 2015, there was a significantly greater proportion of the average time observed with no sentinel than expected [estimate = 0.110, 95% CI = (0.0299, 0.191), $df = 8$, $P = 0.0133$] (Fig. 1).

Across both years, the average proportion of time observed with multiple sentinels overlapping was significantly greater than expected for combinations of four birds [estimate = 0.0676, 95% CI = (− 0.000904, 0.134), $df = 6$, $P = 0.0478$] (Fig. 2). Across both years, the average observed proportion of time with multiple sentinels overlapping was significantly less than expected for combinations of two birds [estimate = − 0.125, 95% CI = (− 0.169,

Fig. 1 Difference between the average observed and expected proportion of time (*y*-axis) with no sentinel. *x*-axis represents the average proportion of time with no sentinel. *Triangles* represent social groups observed in 2015 while *circles* represent groups observed in 2002. The *dotted line* represents a difference of zero (i.e. observed = expected)
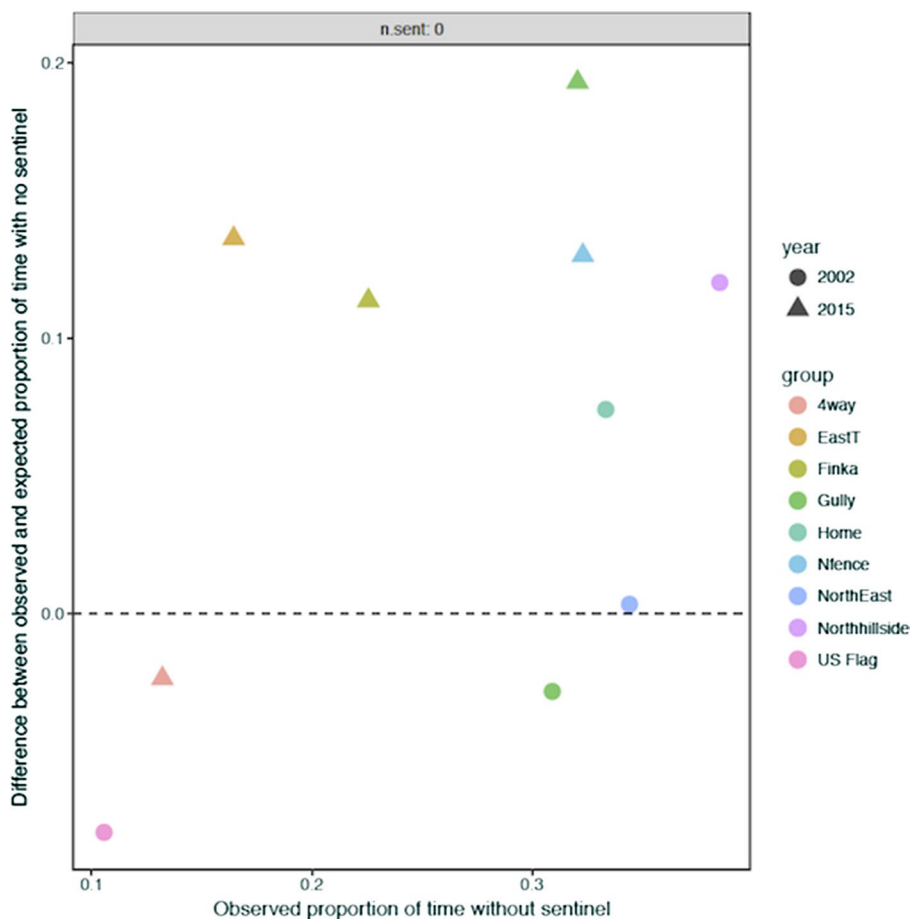
Fig. 2 Difference between the average observed and expected proportion of time (*y*-axis) for from two to five sentinels overlapping. *x*-axis represents the average observed proportion of time with overlapping sentinels. *Triangles* represent social groups observed in 2015 while *circles* represent groups in 2002. The *dotted line* represents a difference of zero (i.e. observed = expected). *Asterisk* indicates a significant difference between average observed and expected values for overlap between multiple sentinels
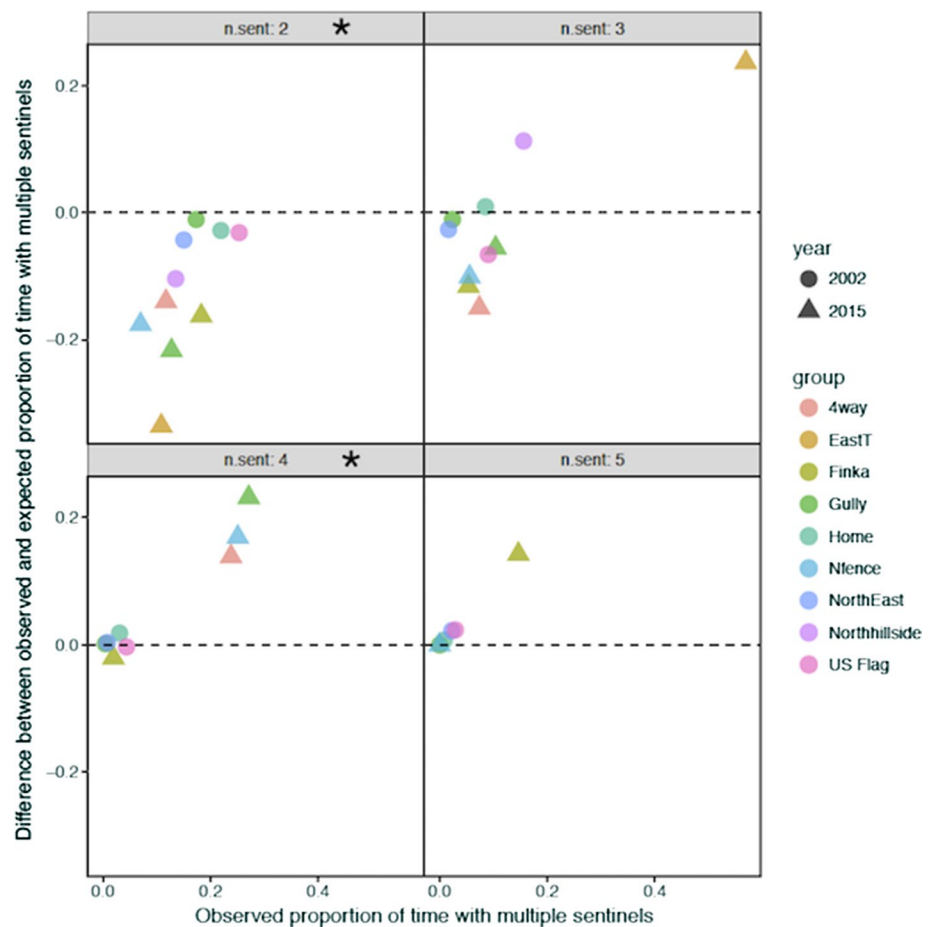
Table 1 Linear mixed model (LMM) results used to examine differences between observed and expected proportion of time with multiple sentinels (i.e. overlap between two and five sentinels) for 2002

Fixed effect estimate	95% CI	*df*	*P*-value
Overlap between two sentinels			
Type − 0.0438	− 0.0881, 0.0001616	4	0.0520
Overlap between three sentinels			
Type 0.00353	− 0.0794, 0.0865	4	0.912
Overlap between four sentinels			
Type 0.00519	− 0.00969, 0.0201	3	0.348
Overlap between five sentinels			
Type 0.0133	− 0.00515, 0.0317	3	0.106

For each LMM the sole fixed effect is Type (i.e. observed or expected). Average proportion of time with multiple sentinels overlapping was the response variable

CI Confidence interval

Table 2 LMM results used to examine differences between observed and expected proportion of time with multiple sentinels (i.e. overlap between two and five sentinels) for 2015

Fixed effect estimate	95% CI	*df*	*P*-value
Overlap between two sentinels			
Type − 0.206	− 0.303, − 0.110	4	< 0.01
Overlap between three sentinels			
Type − 0.0375	− 0.232, 0.157	4	0.621
Overlap between four sentinels			
Type 0.130	− 0.0412, 0.301	3	0.0944
Overlap between five sentinels			
Type 0.0713	− 0.835, 0.978	1	0.500

For each LMM the sole fixed effect is Type (i.e. observed or expected). Average proportion of time with multiple sentinels overlapping was the response variable. For abbreviations, see Table 1

− 0.0805), *df* = 8, *P* < 0.01] (Fig. 2). Across both years, there was also no significant difference between the average observed and expected proportion of time for combinations of three birds [estimate = − 0.0170, 95% CI = (− 0.103, 0.0685), *df* = 8, *P* = 0.659], and five birds

[estimate = 0.0423, 95% CI = (− 0.0195, 0.104), *df* = 4, *P* = 0.130] (Fig. 2).

In 2002, there was no significant difference between the average observed and expected proportion of overlap time for combinations of overlap between two and five birds (Table 1; Fig. 2).

In 2015, there was no significant difference between the average observed and expected proportion of overlap time with multiple sentinels for combinations of three, four, and five birds, although there was a trend for greater than expected combinations of four birds (Table 2; Fig. 2). The average observed proportion of time with multiple sentinels overlapping was significantly less than expected for combinations of two birds (Table 2; Fig. 2).

Smooth-billed Anis were not observed to use unique vocalizations to signal sentinel presence or to signal the end of a sentinel bout.

Discussion

Smooth-billed Anis did not demonstrate a coordinated sentinel system despite the benefits associated with social behaviour such as cooperative nest defence or referential alarm-calling systems. Most Smooth-billed Ani social groups were observed to have a greater proportion of time without a sentinel than expected indicating a lack of coordination.

Most social groups tended to have groups of four sentinels for a greater proportion of time than expected, but not for other numbers of simultaneous sentinels. On the other hand, social groups were observed to have pairs of sentinels for a significantly lower proportion of time than expected. One possible explanation for this trend of overlap in four sentinels versus pairs may be related to an imminent/immediate predatory threat whereby probability of capture is high. This may cause the majority of individuals in social groups to become vigilant sentinels. Another possible reason for this pattern of overlap may be linked to multiple individuals reaching a satiated state. In these circumstances, individuals may choose to assume sentinel behaviour for a better vantage point. Overall, these results also indicate a lack of coordination (as defined by Bednekoff 2015; McGowan and Woolfenden 1989).

Smooth-billed Anis did not appear to use any unique vocalizations that might aid coordination of sentinel bouts as observed in other species (Gaston 1977; Manser 1999; Hollen et al. 2008). The absence of such vocalizations, however, has been observed in coordinated sentinel systems (e.g. Florida-Scrub Jay, Bednekoff et al. 2008) suggesting that the evolution of coordinated sentinel behaviour may not be dependent on such vocal signals.

The lack of coordinated sentinel behaviour in Smooth-billed Ani social groups may be attributed to a variety of factors. Low relatedness among adults in social groups (Quinn and Startek-Foote 2000; Robertson et al. 2017) may explain the absence of a coordinated system. Kin selection has been suggested to be one of the drivers behind coordinated vigilance (Clutton-Brock et al. 1999). Delayed dispersal of kin may allow for small and stable long-lived groups to form

(Bednekoff 1997) whereby the costs of monitoring conspecifics is low and the benefits of coordination high (Ward 1985). Kin selection may also be a strong evolutionary force in promoting coordination where kin groups rely on the survival of young-of-the-year for reproductive success or territory acquisition, as seen in some helper-at-the-nest cooperative breeders [e.g. Florida Scrubjays (Woolfenden and Fitzpatrick 1984)]. However, since Smooth-billed Anis typically form groups of unrelated adults (Quinn and Startek-Foote 2000; Robertson et al. 2017), kin selection benefits promoting sentinel behaviour are likely non-existent except during periods when fledglings are with the group. Furthermore, empirical and theoretical studies have shown that kin selection may not be necessary for the evolution of coordinated sentinel behaviour (Bednekoff 1997; Clutton-Brock et al. 1999; Wright et al. 2001b; Bednekoff 2003).

Another character influencing the evolution and maintenance of a coordinated system is the stability of group composition across years. Coordination of sentinel behaviour has been suggested to be an example of reciprocal altruism (Bednekoff 1997; Clutton-Brock et al. 1999). This is likely the case for highly social species, whereby individuals are able to recognize one another to keep track of sentinel bouts and detect defectors from sentinel duty (Blumstein 1999). Continuous cooperation among the same individuals can promote reciprocity that leads to coordinated vigilance (Brandl and Bellwood 2015). Indeed, coordinated vigilance is known to be favoured when group composition is stable as this makes cheating unlikely (Wickler 1985). Furthermore, by maintaining consistent group membership, this may also confer greater reliability of alarm calls of sentinels as a result of familiarity versus unfamiliar or unreliable individuals/signals (Hare and Atkins 2001), facilitating more effective sentinel coordination over time. Unstable group composition in Smooth-billed Anis persists as social groups that form during the breeding season typically dissolve into large loose flocks at the end of the season. These foraging flocks roam freely as territory boundaries become blurred (Quinn and Startek-Foote 2000). Come the following breeding season, group composition and territory boundaries are often different. While fledglings and adults may occasionally remain on natal/breeding territory between breeding seasons (Quinn and Startek-Foote 2000), group membership often changes as juvenile retention is low (Robertson 2016). Furthermore, flexibility in group composition/size may also arise as Smooth-billed Anis are not obligatory cooperative breeders and can nest as lone pairs (Quinn and Startek-Foote 2000). Indeed, group membership was not consistent across years for the majority of social groups (see Appendix A, Table A1). Such dynamic group composition across years in Smooth-billed Ani may be a pertinent barrier for the evolution of coordinated sentinel behaviour predicated on reciprocal altruism.

Arguably the length of a breeding season [~ 4 months (as per length of rainy season)] could provide sufficient time for a reciprocal altruistic system of coordinating sentinel bouts to evolve as group membership is stable during this period (Quinn and Startek-Foote 2000). The time required for individuals to remain together that would facilitate a coordinated sentinel system, however, remains unknown. Species in which a coordinated sentinel system has been tested and positively identified (i.e. Florida Scrub-Jays and Meerkats, *Suricata suricatta*), form long-lived, stable, kin groups whereby offspring may delay dispersal for up to 2 and 5 years, respectively (Woolfenden and Fitzpatrick 1984; Clutton-Brock et al. 2008). In both species, some individuals may remain on the natal territory and eventually inherit dominant breeding positions (Woolfenden and Fitzpatrick 1978, 1984; Clutton-Brock et al. 2008). Based on these studies, the stability of group composition/membership across multiple years could facilitate a coordinated system via reciprocal altruism. Such stability in group membership and composition across that time scale is lacking in our study species.

In conclusion, we show that Smooth-billed Anis do not appear to perform coordinated sentinel behaviour despite their use of referential alarm calls and vigilant behaviour. However, given our small sample size, further study is warranted. Some environmental and behavioural factors associated with Smooth-billed Anis might favour the evolution of a coordinated sentinel system, while other ecological and life history traits may hinder its evolution. This research demonstrates the importance of quantitative testing of coordination to help distinguish coordinated sentinel systems/behaviour from apparent sentinel systems/behaviour.

References

Bednekoff PA (1997) Mutualism among safe, selfish sentinels: a dynamic game. Am Nat 150:373–392. https://doi.org/10.1086/286070

Bednekoff PA (2003) Florida scrub-jays (*Aphelcoma coerulescens*) are sentinels more when well-fed (even with no kin nearby). Ethology 109:895–903. https://doi.org/10.1046/j.01791613.2003.00926.x

Bednekoff PA (2015) Sentinel behavior: a review and prospectus. Adv Study Behav 47:115–141. https://doi.org/10.1016/bs.asb.2015.02.001

Bednekoff PA, Bowman R, Woolfenden GE (2008) Do conversational gutterals help Florida scrub-jays coordinat their sentinel behaviour? Ethology 114:313–317

Blumstein DT (1999) Selfish sentinels. Science 284:1633–1634. https://doi.org/10.1126/science.284.5420.1633

Brandl SJ, Bellwood DR (2015) Coordinated vigilance provides evidence for direct reciprocity in coral reefs. Sci Rep 5:14556. https://doi.org/10.1038/srep14556

Clutton-Brock TH, O'Riain MJ, Brotherton PNM, Gaynor D, Kansky R, Griffin AS, Manser M (1999) Selfish sentinels in cooperative mammals. Science 284:16401644. https://doi.org/10.1126/science.284.5420.1640

Clutton-Brock TH, Hodge SJ, Flower TP (2008) Group size and the suppression of subordinate reproduction in Kalahari meerkats. Anim Behav 76:689–700. https://doi.org/10.1016/j.anbehav.2008.03.015

Davis DE (1940) Social nesting habits of the Smooth-billed Ani. Auk 57(2):179–218. https://doi.org/10.2307/4078745

Ekman J, Dickinson JL, Hatchwell BJ, Griesser M (2004) Delayed dispersal. In: Koenig WD, Dickinson JL (eds) Evolution and ecology of cooperative breeding in birds. Cambridge University Press, Cambridge, pp 35–47

Gaston AJ (1977) Social-behavior within groups of Jungle Babblers (*Turdoides striatus*). Anim Behav 25:828–848. https://doi.org/10.1016/0003-3472(77)90036-7

Grieves LA, Logue DM, Quinn JS (2014) Joint-nesting Smooth-billed Anis, *Crotophaga ani*, use a functionally referential alarm call system. Anim Behav 89:214–221. https://doi.org/10.1016/j.anbehav.2014.01.008s

Hare JF, Atkins BA (2001) The squirrel that cried wolf: reliability detection by juvenile Richardson's Ground Squirrels (*Spermophilus richardsonii*). Behav Ecol Sociobiol 51:108112. https://doi.org/10.1007/s002650100414

Hollen LI, Bell MB, Radford AN (2008) Cooperative sentinel calling? Foragers gain increased biomass intake. Curr Biol 18:576–579. https://doi.org/10.1016/j.cub.2008.02.078

Komdeur J (1995) Facultative sex ratio bias in the offspring of Seychelles Warblers. Proc R Soc B Biol Sci 263:661–666. https://doi.org/10.1098/rspb.1996.0099

Loflin RK (1983) Communal behaviors of the Smooth-billed Ani (*Crotophaga ani*). Dissertation, University of Miami

Manser MB (1999) Response of foraging group members to sentinel calls in Suricates, *Suricata suricatta*. Proc R Soc B Biol Sci 266:1013–1019. https://doi.org/10.1098/rspb.1999.0737

McGowan KJ, Woolfenden GE (1989) A sentinel system in the Florida Scrub Jay. Anim Behav 37:1000–1006. https://doi.org/10.1016/0003-3472(89)90144-9

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: linear and nonlinear mixed effects models. https://cran.rproject.org/web/packages/nlme/nlme.pdf. Accessed Aug 2016

Quinn JS, Startek-Foote JM (2000) Smooth-billed Ani. In: Poole A, Gill F (eds) The birds of North America. Academy of Natural Sciences, Philadelphia, p 539

Rasa OAE (1986) Coordinated vigilance in Dwarf Mongoose family groups: the 'watchman song' hypothesis and the costs of guarding. Ethology 71:340–344. https://doi.org/10.1111/j.1439-0310.1986.tb00598.x

R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.Rproject.org/. Accessed Aug 2016

Ridley AR, Raihani NJ, Bell MBV (2010) Experimental evidence that sentinel behaviour is affected by risk. Biol Lett 6:445–448. https://doi.org/10.1016/j.anbehav.2012.10.017

Ridley AR, Nelson-Flower MJ, Thompson AM (2013) Is sentinel behaviour safe? An experimental investigation. Anim Behav 85:137–142. https://doi.org/10.1016/j.anbehav.2012.10.017

Robertson JK (2016) Reproductive competition and skew in a joint-nesting cuckoo. Thesis, McMaster University

Robertson JK, Cladwell JR, Grieves LA, Samuelsen A, Schmaltz GS, Quinn JS (2017) Male parental effort predicts reproductive contribution in the joint-nesting, Smooth-billed Ani (*Crotophaga ani*). J Ornithol. https://doi.org/10.1007/s10336-017-1522-z

Schmaltz G, Quinn JS, Lentz C (2008) Competition and waste in the communally breeding Smooth-billed Ani: effects of group size on egg-laying behaviour. Anim Behav 76:153–162. https://doi.org/10.1016/j.anbehav.2007.12.018

Sorato E, Gullett PR, Griffith SC, Russell AF (2012) Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species. Anim Behav 84:823–834. https://doi.org/10.1016/j.anbehav.2012.07.003

Ward PI (1985) Why birds in flocks do not coordinate their vigilance periods. J Theor Biol 114:383–385

Wickler W (1985) Coordination of vigilance in bird groups: the watchman's song hypothesis. J Comp Ethol 69:250–253. https://doi.org/10.1111/j.1439-0310.1985.tb00150.x

Woolfenden GE, Fitzpatrick JW (1978) The inheritance of territory in group breeding birds. Bioscience 28:104–108. https://doi.org/10.2307/1307423

Woolfenden GE, Fitzpatrick JW (1984) The Florida Scrub Jay: demography of a cooperative breeding bird. Princeton University Press, Princeton

Wright J, Berg E, de Kort SR, Khazin V, Makalakov AA (2001a) Safe selfish sentinels in a cooperative bird. J Anim Ecol 70:1070–1079. https://doi.org/10.1046/j.0021-8790.2001.00565.x

Wright J, Maklakov AA, Khazin V (2001b) State-dependent sentinels: an experimental study in the Arabian Babbler. Proc R Soc B Biol Sci 268:821–826. https://doi.org/10.1098/rspb.2000.1574

Yasukawa K, Cockburn A (2009) Antipredator vigilance in cooperatively breeding Superb Fairy-wrens (*Malurus cyaneus*). Auk 126:147–154. https://doi.org/10.1525/auk.2009.08074

Affiliations

Jing Sheng Hing[1] · Gregory Schmaltz[2] · James S. Quinn[1]

[1] Department of Biology, McMaster University, Life Sciences Building, 1280 Main Street West, Hamilton, ON L8S 4K1, Canada

[2] University of the Fraser Valley, 33844 King Road, Abbotsford Campus, B328, Abbotsford, BC V2S 7M8, Canada