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# Effects of Chimpanzee (*Pan troglodytes*) Hunting Seasonality and Red Colobus (*Piliocolobus badius*) Association on Diana Monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire

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**Abstract** Polyspecific associations occur when species overlap in their environment by chance, converge at common resources, or in response to predation pressure. However, because larger groups may themselves attract the attention of predators, species forming associations must balance the costs and benefits of comingling. Experimental and observational research suggests red colobus (*Piliocolobus badius*) associate with Diana monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire in response to seasonally shifting predation pressure from chimpanzees (*Pan troglodytes verus*). Research on this system has focused on immediate behavioral effects of comingling by red colobus and Diana monkeys. We expand on these analyses and explore longer-term changes in Diana monkey behavior. We use scan samples ($N$ = 7025) collected on three Diana monkey groups over 5 years ($N$ = 380 days) to assess differences in diet, activity budget, and strata use in relation to associating with red colobus and chimpanzee hunting seasonality and test for interaction effects between these two variables. We found limited evidence showing Diana monkeys make more than ephemeral behavioral changes in response to comingling with red colobus during chimpanzees' hunting season (September–November). Synergistic effects of association and hunting season include expanded use of the main canopy, decreased fruit consumption, and increased invertebrate consumption. We find little evidence indicating Diana monkeys minimize behaviors that increase risk of predation from chimpanzees while associated with red colobus during the season when chimpanzees hunt most

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often. We conclude that when there are few member costs to forming mixed groups, participating species may tolerate associations even without accruing any benefits.

**Keywords** *Cercopithecus diana* · *Piliocolobus badius* · Mixed-species groups · Polyspecific association · Predation · Strata use

## Introduction

Members of the order Primates form polyspecific associations relatively frequently and commonly (e.g., Burton and Chan 1996; Chapman and Chapman 2000; Cords 1990; Gartlan and Struhsaker 1972; Gautier-Hion *et al.* 1983; McGraw and Zuberbühler 2008; Norconk 1990; Oates and Whitesides 1990; Terborgh 1990; Tutin *et al.* 1997; Waser 1982). Understanding factors leading to the formation and maintenance of such associations has been a central concern for ecologists, and most associations studied to date are attributable to either random overlaps in space, convergences on common resources, or responses to predator pressure (Stensland *et al.* 2003; Terborgh 1990; Waser 1984). Participation in a mixed-species group increases group size, which relaxes per capita vigilance and dilutes the risk of predation to any one individual (Pulliam and Caraco 1984; Stanford 2002). However, larger groups formed by multiple species coming together may attract predators, so participating species must balance the costs and benefits of polyspecific association (Stanford 2002).

Researchers have studied mixed-species associations of monkeys in Taï National Park for >30 years (Galat and Galat-Luong 1985). At Taï, associations range in duration from fleeting to virtually permanent (McGraw and Zuberbühler 2008). Diana monkeys (*Cercopithecus diana*) most commonly participate in mixed-species groups and are a nuclear species because of their value to other taxa as sentinels (Buzzard 2010; McGraw and Zuberbühler 2008). Diana monkeys rapidly detect and respond to terrestrial and aerial predators (Buzzard 2010; McGraw and Zuberbühler 2008). When associated with other monkeys, they alarm call first 49% of the time—more than twice as much as the other guenon taxa (*C. campbelli:* 21%; *C. petaurista*: 18%) or other sympatric cercopithecids (*Colobus polykomos*, *Piliocolobus badius*, *Procolobus verus*, *Cercocebus atys*: 12% in total) (Buzzard 2010). The dynamics of their associations with other taxa in Taï shows that association costs and benefits for Diana monkeys vary significantly because partner species comingle for different timespans, during different seasons, and for different reasons (e.g., Buzzard 2006a, 2006b, 2006c, 2010; Buzzard and Eckardt 2007; Eckardt and Zuberbühler 2004; Kane and McGraw 2017; Korstjens 2001; McGraw and Bshary 2002; McGraw and Zuberbühler 2008; Oates and Whitesides 1990).

The most intriguing comingling of monkey taxa at Taï is that of Diana monkeys and red colobus (*Piliocolobus badius*). These species associate more frequently than predicted by chance (Holenweg *et al.* 1996; Waser 1982, 1984). Diana monkeys and red colobus at Taï occupy distinct feeding niches: Diana monkeys specialize on ripe fruit and invertebrates, while red colobus specialize on young leaves, unripe fruit, and flowers (Wachter *et al.* 1997). They associate more regularly than attraction to common resources can account for and comingling results in no foraging benefit to either species (Korstjens 2001; Wachter *et al.* 1997).

Chimpanzees (*Pan troglodytes verus*) in Taï National Park hunt seasonally and cooperatively (Boesch 1994; Boesch and Boesch 1989; Boesch and Boesch-Achermann 2000). The Taï chimpanzees primarily hunt vertebrates, with a particular focus on the colobines (93% of successful hunts between 1984 and 1995; Boesch and Boesch-Achermann 2000). Predation pressure on red colobus is intense: between 1984 and 1995, red colobus composed 80% of chimpanzee prey at Taï and offtake was estimated at 3–8% of the red colobus population annually (Boesch and Boesch-Achermann 2000). Chimpanzee hunting frequency and success improve during the wet season, with hunts occurring at least daily between September and November compared to weekly hunts the rest of the year (Boesch and Boesch-Achermann 2000). Consequently, chimpanzee hunting pressure on red colobus fluctuates seasonally: Boesch (1994) estimated that chimpanzees kill 72 red colobus during the hunting season, compared to 53 the other 9 months of the year.

Experimental and observational research suggests that red colobus initiate polyspecific associations with Diana monkeys to counter hunting pressure from chimpanzees and that they benefit from Diana monkeys' sentinel capabilities (Bshary and Noë 1997a, 1997b; Buzzard 2010; Höner *et al.* 1997; Noë and Bshary 1997). Association frequencies between the two cercopithecid taxa peak during the chimpanzees' hunting season, and when the monkey species comingle, red colobus 1) expand their canopy use and visit lower strata more often than when alone, 2) engage in fewer vigilance behaviors, and 3) are more likely to be exposed from the front or below (Bshary and Noë 1997b; Noë and Bshary 1997). Field experiments also demonstrate that unassociated red colobus groups seek out and mix with nearby Diana groups in response to playbacks of chimpanzee vocalizations (Bshary and Noë 1997a). In the presence of red colobus, Diana monkeys use the main and upper canopy more extensively, and are more exposed from the front, rear, and above (Bshary and Noë 1997b). Although Taï chimpanzees preferentially hunt red colobus, they do occasionally hunt Diana monkeys (Boesch and Boesch-Achermann 2000; Kane and Gnepa 2016). Diana monkeys respond to chimpanzees' presence or vocalizations by ascending to the main canopy and becoming quiet and cryptic; they also occasionally alarm call (Buzzard 2010; McGraw and Zuberbühler 2008; Zuberbühler *et al.* 1999).

Boesch and colleagues contend that monkey-hunting chimpanzees target red colobus groups by using audible cues from Diana monkeys. They argue that chimpanzees move toward and hunt red colobus associated with Diana monkeys more frequently than unassociated red colobus (Boesch 1994; Boesch and Boesch-Achermann 2000). If Diana monkey vocalizations attract chimpanzees that hunt when red colobus are present, we would predict shifts in Diana monkey maintenance behaviors, strata use, and diet to occur in response to red colobus presence during chimpanzees' hunting season. Though comingling occurs outside the chimpanzee hunting season, Diana monkeys mixed with red colobus during the hunting season should be at greatest risk.

Here we use 5 years of scan samples ($N = 7025$) to examine the behavior of Diana monkeys 1) when mixed with red colobus and 2) during the chimpanzee hunting season. Because Diana monkeys associate with red colobus both in and outside the hunting season, we evaluate a third context: if the presence of red colobus and the hunting season independently lead to changes in Diana monkey behavior, the combined effect of these may be greater than the effect of either condition alone. Therefore, we examine possible synergistic effects of association with red colobus during the hunting

season, predicting the presence of red colobus and the seasonality of chimpanzee hunting lead to shifts in Diana monkey behavior, diet, and strata use. We predict that Diana monkeys associated with red colobus during the hunting season spend more time traveling (avoiding hunting chimpanzee groups) and resting (remaining cryptic in response to chimpanzees) and less time foraging or socializing. We predict that they spend less time exposed in lower strata and more time in the upper canopy. Because Diana monkeys and red colobus do not share an overlapping feeding niche, we do not predict that dietary differences will result as a function of associating during the hunting season.

## Methods

### Study Site and Species

We collected data in the study area of the Taï Monkey Project in Taï National Park, Côte d'Ivoire (6°20′N to 5°10′N, 4°20′W to 6°50′W). The park is in southwestern Côte d'Ivoire ca. 25 km from the Liberian border, and is composed of 330,000 ha of protected forest surrounded by a matrix of cocoa and rubber plantations and villages. The forest receives a mean of 1893 mm of rainfall per year during two wet seasons (April–June; September–October) and two dry seasons (November–March, July–August) (Anderson *et al.* 2005). Taï National Park supports a diverse array of wildlife, including nine anthropoid taxa: four guenons (Diana monkeys: *Cercopithecus diana*; Campbell's monkeys: *C. campbelli*; lesser spot-nosed guenons: *C. petaurista*; greater spot nosed guenons: *C. nictitans*), three colobines (black-and-white colobus: *Colobus polykomos*; olive colobus: *Procolobus verus*; red colobus: *Piliocolobus badius*), one terrestrial mangabey (*Cercocebus atys*), and the western chimpanzee (*Pan troglodytes verus*) (McGraw *et al.* 2007).

### Data Collection

Ferdinand Belé, a field assistant of the Taï Monkey Project, collected data between July 2004 and July 2009. He observed three habituated groups of Diana monkeys ranging within the project study grid. Each group consisted of one adult male, 7–13 adult females, and 3–7 subadults and juveniles (Buzzard and Eckardt 2007). We sampled groups on a rotating basis and followed each group for 4–7 days per month. Every morning, F. Bele located the focal group in its sleeping tree and followed it until group members entered a sleeping tree for the night, generally from 07:00 to 18:00 h. He took scan samples every 30 min, with each scan lasting 10 min because of group spread and visibility constraints (Altmann 1974). During scans, he moved through the group and recorded the age and sex class, vertical position, and behavior of all visible adults and subadults. If sex and age could not be determined, he included individuals in the scan classified as indeterminate age and sex. Vertical position was determined on a five-point scale: 0 = ground, 1 = shrubbery layer, 2 = understory, 3 = main canopy, 4 = emergent layer (McGraw 1996). He recorded behaviors including foraging, locomotion, resting, and social interactions. He

also recorded food type (e.g., fruit, leaf, invertebrate) when individuals foraged. He also recorded the presence of spatially comingled (within 0–25 m) species associated with the focal Diana monkey group.

### Data Analysis

We treated each scan sample as a single data point, and calculated the proportion of individuals performing different behaviors, located at various strata, and feeding on different food types during each scan. We pooled data for the three Diana monkey groups after determining groups did not differ significantly in strata use or gross diet, and because each group regularly associated with red colobus (Bshary and Noë 1997b; Höner *et al.* 1997; Kane and McGraw 2017). We followed Noë and Bshary (1997) in dividing our data seasonally: the hunting season (September–November), dry season 1 (December–February), wet season 1 (March–May), and dry season 2 (June–August). We further divided seasonal data by association state: e.g., associated with red colobus during the hunting season, not associated with red colobus during the hunting season, associated during dry season 1, not associated during dry season 1, etc. We report data as seasonal means with 95% confidence intervals.

We visually inspected our data for normality using a Q–Q plot, and found data distributed approximately normally. ANOVA are robust to heterogeneity of variance at large sample sizes; because of our large sample size ($N = 7025$ scan samples), equality of group size, and approximately normal distribution, we used a two-way ANOVA (Jaccard 1998). We tested for interaction effects of season and association on Diana monkeys' activity budget, strata use, and diet (e.g., whether there was an effect of association with red colobus on time spent foraging during different seasons). When we found a statistically significant interaction effect, we tested for simple main effects of association in each season (Keppel and Wickens 2004). In other words, a significant interaction effect indicated that association with red colobus monkeys affected Diana monkey behavior differently depending on the season; testing for simple main effects of association allowed us to examine the impact of association during each season. We report whether there was a significant interaction effect and, if there was, whether association had a significant effect on the dependent variable during the hunting season. The $\alpha$-level was set at 0.05. We used Bonferroni's correction to adjust the $\alpha$-level for post hoc comparisons when necessary and conducted statistical tests in SPSS 24.0.

**Data Availability** The datasets analyzed during the current study are available from the corresponding author on reasonable request.

## Ethical Note

Data collection met the guidelines of the American Society of Primatologists' principles for the ethical treatment of nonhuman primates and was approved by the Ohio State University IACUC and permit-granting bodies in Côte d'Ivoire.

The authors declare that they have no conflicts of interest.

## Results

We analyzed 7025 scan samples collected on 380 days during 21 seasons between July 2004 and July 2009: 23.5% during the hunting season (September–November), 26.2 during dry season 1 (December–February), 31.5% during wet season 1 (March–May), and 18.8% during dry season 2 (June–August). Diana monkeys associated with red colobus during 64.9% of scans, and were not associated during 35.1% of scans. Diana monkeys were less likely to associate with red colobus than expected during the chimpanzees' hunting season, and more likely than expected to associate with red colobus during dry season 2 (June–August) (Fig. 1; $\chi^2(3) = 28.402$, $P < 0.001$). We found no significant effects of the interaction of association state and season on Diana monkeys' activity budgets (Table I, Fig. 1), including time spent locomoting, resting, socializing, or foraging.

Association with red colobus and hunting season yielded some significant interaction effects on Diana monkeys' strata use (Tables I and II, Fig. 2). During the hunting season, Diana monkeys used the main canopy significantly more when associated with red colobus (70.5%, 95% CI (68.3–72.8)) than when they were not associated (65.4%, 95% CI (62. 6–68.8)). However, there was no significant effect of the interaction of

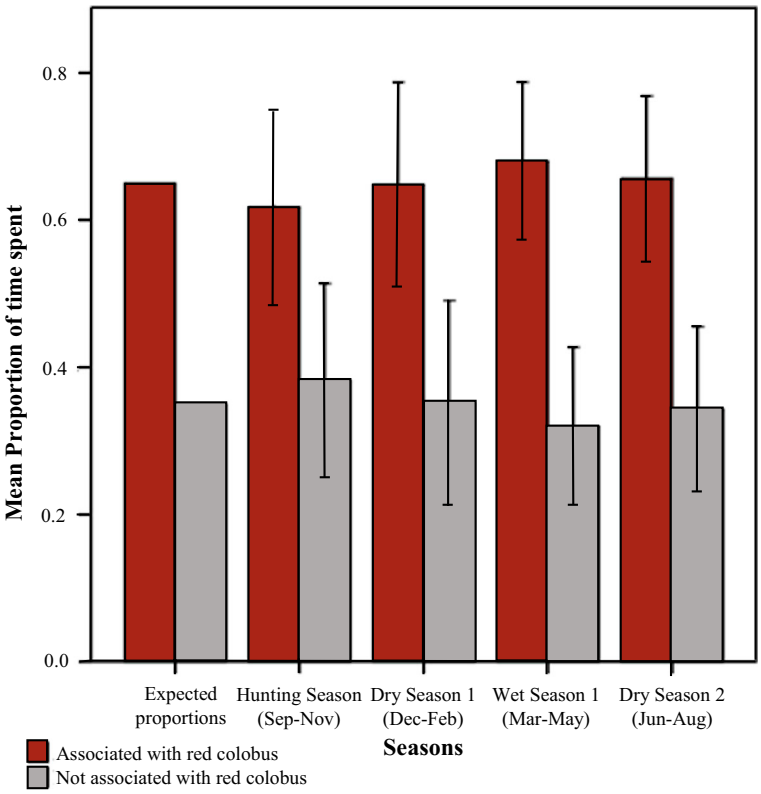


**Fig. 1** The expected and observed mean seasonal proportions of association between Diana monkeys (*Cercopithecus diana*) and red colobus (*Piliocolobus badius*) in Taï National Park, Côte d'Ivoire between July 2004 and July 2009. Error bars indicate 95% confidence intervals.

**Table I** Results of ANOVAs testing for an interaction effect of hunting season and association with red colobus (*Piliocolobus badius*) on Diana monkey (*Cercopithecus diana*) activity, strata use, and diet in Taï National Park, Côte d'Ivoire between July 2004 and July 2009

| Interaction effect of hunting season and red colobus comingling on: | *F*-statistic | Degrees of freedom | *P*-value |
|---|---|---|---|
| Time spent in: | | | |
| Locomotion | 1.11 | 3, 6996 | 0.35 |
| Resting | 0.91 | 3, 6996 | 0.43 |
| Foraging | 0.95 | 3, 6996 | 0.41 |
| Social behavior | 1.19 | 3, 6996 | 0.31 |
| Time spent in the: | | | |
| Ground level | 1.07 | 3, 6996 | 0.36 |
| Shrubbery layer | 0.49 | 3, 6996 | 0.69 |
| **Understory** | **4.68** | 3, 6996 | **0.01** |
| **Main canopy** | **7.84** | 3, 6996 | **0.01** |
| Emergent laver | 0.17 | 3, 6996 | 0.92 |
| Time spent eating: | | | |
| **Fruit** | **10.98** | 3, 3712 | **<0.01** |
| **Invertebrates** | **5.88** | 3, 3712 | **<0.01** |
| **Leaves** | **5.40** | 3, 3712 | **0.01** |

Variables with a significant interaction effect are in **bold**

association and season on time spent on the ground, in the shrubbery layer, or in the emergent layer. There was a significant interaction effect of season and association on Diana monkeys' use of the understory; however, this effect was not significant during the hunting season.

We found significant interaction effects of association with red colobus and hunting season on Diana monkey diets (Tables I and II, Fig. 3). During the hunting season, Diana monkeys ate significantly less fruit when associated with red colobus (59.4%, 95% CI (55.7–63.1)) than when not associated (74.5%, 95% CI (69.9–79.1)). By contrast, during the hunting season Diana monkeys ate significantly more invertebrates when associated with red colobus (35.4%, 95% CI (31.9–38.9)), and fewer invertebrates when not associated (27.9%, 95% CI (23.3–32.4)). Though there was a significant interaction effect of season and association on leaf consumption, during the hunting season there was no difference in consumption when groups were (5.3%, 95% CI (3.6–6.9%)) or were not associated with red colobus (3.8%, 95% CI (1.7–6.0%)) (Fig. 4).

## Discussion

We found little evidence to support the hypothesis that Diana monkeys change their behavior or strata use in response to associating with red colobus when chimpanzees are most likely to be hunting. Because of our large sample sizes, some analyses may have yielded statistically significant results with no biological relevance (Nakagawa

**Table II** Results of ANOVAs testing for a simple main effect of association with red colobus (*Piliocolobus badius*) during different seasons on Diana monkeys' (*Cercopithecus diana*) use of the understory and main canopy, and consumption of fruit, invertebrates and leaves in Taï National Park, Côte d'Ivoire, between July 2004 and July 2009

| Simple main effects of association with red colobus on: | *F*-statistic | Degrees of freedom | *P*-value |
|---|---|---|---|
| Use of the understory during the: | | | |
| Hunting season (Sep–Nov) | 1.78 | 1, 6996 | 0.18 |
| **Dry season 1 (Dec–Feb)** | **22.23** | 1, 6996 | **<0.01** |
| Wet season 1(Mar–May) | 0.59 | 1, 6996 | 0.44 |
| **Dry season 2(Jun–Aug)** | **25.83** | 1, 6996 | **<0.01** |
| Use of the main canopy during the: | | | |
| **Hunting season (Sep–Nov)** | **7.84** | 1, 6996 | **0.01** |
| **Dry season 1 (Dec–Feb)** | **18.90** | 1, 6996 | **<0.01** |
| Wet season 1(Mar–May) | 1.19 | 1, 6996 | 0.28 |
| **Dry season 2 (Jun–Aug)** | **39.19** | 1, 6996 | **<0.01** |
| Fruit consumption during the | | | |
| **Hunting season (Sep–Nov)** | **8.40** | 1, 6996 | **<0.01** |
| **Dry season 1 (Dec–Feb)** | **8.60** | 1, 6996 | **<0.01** |
| **Wet season 1 (Mar–May)** | **8.65** | 1, 6996 | **<0.01** |
| **Dry season 2 (Jun–Aug)** | **7.41** | 1, 6996 | **0.01** |
| Invertebrate consumption during the: | | | |
| **Hunting season (Sep–Nov)** | **6.54** | 1, 3712 | **0.01** |
| **Dry season 1 (Dec–Feb)** | **10.52** | 1, 3712 | **<0.01** |
| Wet season 1 (Mar–May) | 2.45 | 1, 3712 | 0.12 |
| Dry season 2 (Jun–Aug) | 1.40 | 1, 3712 | 0.24 |
| Leaf consumption during the: | | | |
| Hunting season (Sep–Nov) | 5.40 | 1, 3712 | 0.31 |
| Dry season 1 (Dec–Feb) | 0.01 | 1, 3712 | 0.93 |
| **Wet season 1 (Mar–May)** | **9.81** | 1, 3712 | **<0.01** |
| **Dry season 2 (Jun–Aug)** | **12.62** | 1, 3712 | **<0.01** |

Seasons with a significant simple main effect of association are in **bold**

and Cuthill 2007). Therefore, the fact that we found very few statistically significant differences in Diana monkey behavior during the chimpanzee hunting season in and out of association with red colobus underscores the point that Diana monkey behavior changes very little in response to these variables.

Diana monkeys rarely adjusted their activity budgets as a consequence of associating with red colobus during the chimpanzee hunting season: regardless of association, Diana monkeys locomoted, rested, socialized, and foraged at similar rates. This is consistent with previous reports that Diana monkey ranging behavior is essentially constant in and out of association with red colobus (Holenweg *et al.* 1996; Höner *et al.* 1997). Habitat use also remained remarkably consistent during the hunting season, regardless of association with red colobus. Diana monkeys did not reduce time spent at the lowest forest levels and did not consistently forage in higher and presumably safer

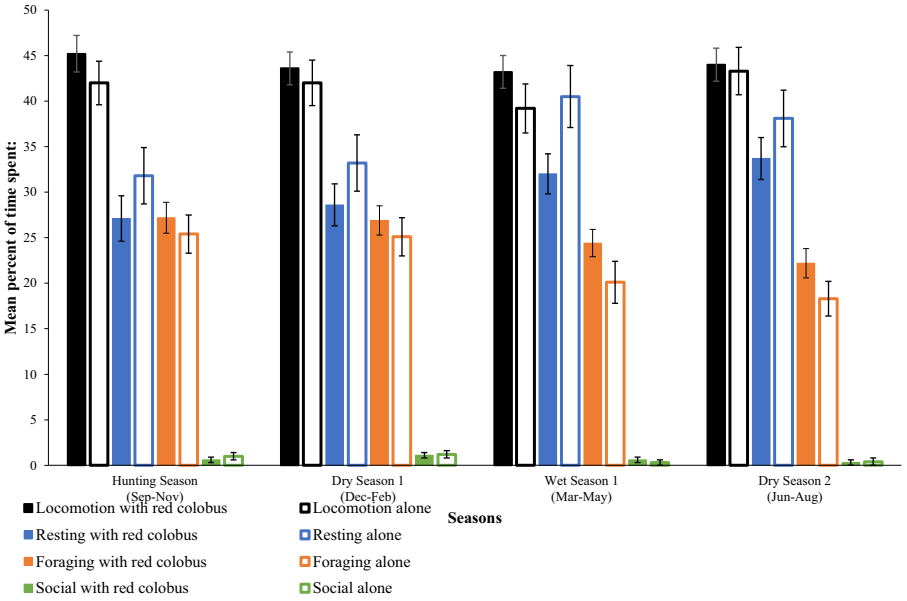


**Fig. 2** Mean seasonal activity budgets of Diana monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire derived from 7025 scan samples collected between July 2004 and July 2009. Solid bars represent Diana monkey behavior while associated with red colobus (*Piliocolobus badius*); empty bars represent Diana monkey behavior while unassociated. Error bars indicate 95% confidence intervals.

forest strata during chimpanzees' hunting season. During the hunting season, Diana monkeys used the main canopy significantly more (5%) when associated with red colobus than when unassociated; however, we are skeptical that this 5% increase represents a meaningful change in Diana monkeys' behavior. It is more instructive to note that Diana monkeys increase their use of the ground during the hunting season relative to the rest of the year, regardless of association with red colobus. Based on safety considerations alone, the fact that Diana monkeys more frequently position themselves close to the ground during the season chimpanzees tend to hunt monkeys is puzzling.

We suspect the explanation for this behavior lies in diet: foraging behavior associated with a single, highly prized fruit species accounts for the significant change in strata use observed during this season. Expanded use of the ground and shrub layers during the hunting season is likely the result of foraging for fruit of *Sacoglottis gabonensis*. This fruit, which composes nearly 20% of the Diana monkey diet annually is eaten primarily between the months of August and October, a period coinciding with the chimpanzees' hunting season (Kane and McGraw 2017). During this period, Diana monkeys forage extensively on fruit of *S. gabonensis* in the main canopy (48% of consumption of *S. gabonensis*) and on fallen fruit eaten either at ground level or in the shrubbery layer (48% of consumption of *S. gabonensis*, Taï Monkey Project (TMP) *unpubl. data*). During the hunting season, more than half of their time at ground level and 10% of their time in the main canopy is dedicated to feeding on these fruits.

Although Diana monkeys did not change the amount of time devoted to foraging when comingled with red colobus during the chimpanzees' hunting season, their diets differed significantly: when associated with red colobus, Diana monkeys ate much less fruit (15%) and more invertebrates (13%). Because fruit is an important source of easily

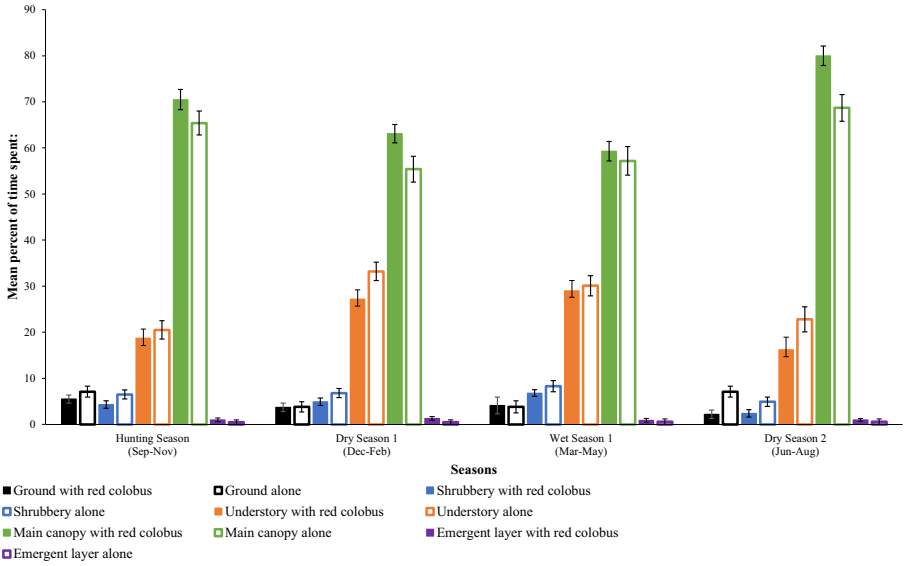


**Fig. 3** Mean seasonal strata use of Diana monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire derived from 7025 scan samples collected between July 2004 and July 2009. Solid bars represent Diana monkey strata use while associated with red colobus (*Piliocolobus badius*); empty bars represent Diana monkey strata use while unassociated. Error bars indicate 95% confidence intervals.

metabolizeable energy, this likely represents a real cost in terms of calorie and energy intake (Danish *et al.* 2006). During the chimpanzees' hunting season, Diana monkeys must balance their efforts to forage for and consume fruit of *Sacoglottis gabonensis* at lower strata, while mitigating the risk of predation—a risk that may be elevated when in association with red colobus. Though Diana monkeys do not increase vigilance behaviors such as scanning when associated with red colobus, they may be more cautious while foraging at ground level (Bshary and Noë 1997b). Many organisms react to elevated predation pressure by increasing vigilance behaviors and more readily giving up a particular food patch before it is completely depleted, with a consequent drop in foraging efficiency (Brown and Kotler 2004). This, combined with less extensive use of the shrubbery layer, may result in lower foraging efficiency during the hunting season when comingled with red colobus. Though there is little dietary overlap between red colobus and Diana monkeys, Diana monkeys may also adjust their travel speed and foraging routes in the presence of red colobus, resulting in fewer visits to preferred feeding trees and concomitant dietary changes (Korstjens 2001). While these dietary differences are significant, the chimpanzees' hunting season falls during a period of high fruit availability and Diana monkeys ate fruit-rich diets during this season regardless of association state (Anderson *et al.* 2005; Kane and McGraw 2017). Thus, despite the dietary consequences of association with red colobus during chimpanzees' hunting season, even when associated with red colobus monkeys (and, perhaps, at their most vigilant), Diana monkeys still eat more ripe fruit during this period than during two other seasons.

Our evaluation of Diana monkey behavior in and out of association with red colobus during the chimpanzee hunting season suggests that these associations incur minimal costs to Diana monkeys during periods when predation pressure from chimpanzees is

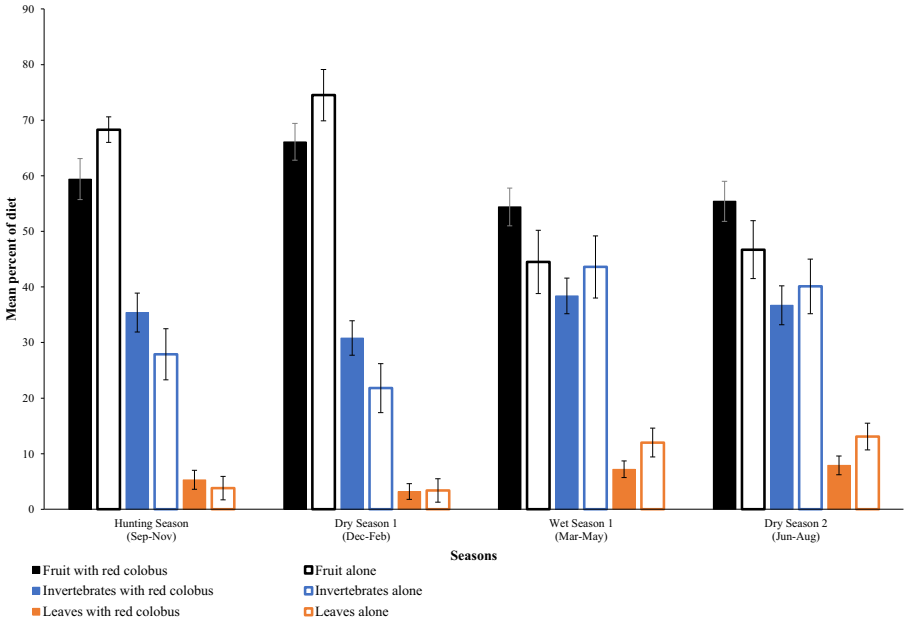


**Fig. 4** Mean seasonal diets of Diana monkeys (*Cercopithecus diana*) in Taï National Park, Côte d'Ivoire derived from 7025 scan samples collected between July 2004 and July 2009. Solid bars represent Diana monkey strata use while associated with red colobus (*Piliocolobus badius*); empty bars represent Diana monkey strata use while unassociated. Error bars indicate 95% confidence intervals.

most significant. Diana monkeys' behavioral changes during this time are few and ephemeral. There is no effect of association on Diana monkeys' activity budget, and they do not change their vigilance behaviors in the presence of red colobus (Bshary and Noë 1997b). They shift their strata use to make greater use of the canopy when associated with red colobus, but they do not spend significantly less time at ground level. We do see a significant reduction in Diana monkeys' fruit consumption during the hunting season while associated with red colobus. However, they still eat more fruit while associated with red colobus during the hunting season than they do between May and August. These findings do not support the hypothesis that Diana monkeys associated with red colobus during the hunting season make significant changes to their behavior in order to mitigate predation risk from chimpanzees. Diana monkeys do not behave as though association with red colobus during chimpanzees' hunting season increases their risk of predation. Because Diana monkeys do not adjust their behavior in response to the formation of polyspecific associations with red colobus, this calls into question the hypothesis that chimpanzees preferentially hunt groups of red colobus monkeys associated with Diana monkeys (Boesch 1994; Boesch and Boesch-Achermann 2000).

## Why Do Diana Monkeys and Red Colobus Form and Maintain Associations in the Taï Forest?

Diana monkeys likely tolerate the presence of red colobus even during periods when hunting pressure from chimpanzees is elevated because there are few costs to the association, and Diana monkeys may actually benefit from these mixed-species groups

(Bshary and Noë 1997a, 1997b; Holenweg *et al.* 1996; Noë and Bshary 1997; Wachter *et al.* 1997). Evidence suggests that the presence of red colobus mitigates pressure from other predators, including crowned eagles, leopards, and perhaps golden cats (Bahaa-el-din *et al.* 2015; Bshary and Noë 1997a, 1997b; Holenweg *et al.* 1996; Noë and Bshary 1997; Wachter *et al.* 1997; Zuberbühler and Jenny 2002). The increased number of individuals resulting from species comingling by itself should improve per capita safety by virtue of the selfish herd effect (Hamilton 1971). Furthermore, red colobus occupy higher forest strata than do Diana monkeys and, by associating with red colobus, Diana monkeys expand their use of the main canopy and emergent layer (Bshary and Noë 1997a; McGraw 1996). Because red colobus generally use higher forest strata than Diana monkeys, the former may provide protection from raptors attacking from above, either in the form of alarm calls, mobbing participants, or simply as passive shields. Such antipredation benefits could explain why Diana monkeys and red colobus associate frequently even outside the chimpanzee hunting season. Unlike chimpanzees, crowned eagles at Taï prey on monkeys year-round (Shultz 2001, 2002; Shultz *et al.* 2004).

Support for this line of reasoning can be found by examining the monkey–predator dynamics and mixed-species associations at other African sites. Diana monkeys, red colobus, and chimpanzees are also sympatric on Sierra Leone's Tiwai Island (Whitesides 1989). At Tiwai, associations between red colobus and Diana monkeys occur very rarely and much less frequently than predicted by chance (Waser 1982, 1984; Whitesides 1989). One Diana monkey group associated with red colobus 3.7% of the time, and another group associated 13.4% of the time (Whitesides 1989). Monkeys at Tiwai experience less predation than their Taï conspecifics, including fewer hunts by chimpanzees, fewer attacks by crowned eagles, and no threat from leopards due to their extirpation (Holenweg *et al.* 1996; Stephan and Zuberbühler 2008; Whitesides 1989; Whitesides *et al.* 1988). The significant reduction in predation pressure very likely curbs the need for associating: because chimpanzees are relatively rare and do not regularly hunt red colobus, red colobus do not seek associations with Diana monkeys. Because eagle attacks are infrequent, Diana monkeys have little impetus to maintain associations with red colobus (Holenweg *et al.* 1996; Stephan and Zuberbühler 2008; Whitesides 1989; Whitesides *et al.* 1988).

In Tanzania's Gombe Stream National Park, chimpanzees (*Pan troglodytes schweinfurthii*) impose significant predation pressure on red colobus (*Piliocolobus tephrosceles*) (Stanford *et al.* 1994). However, Gombe's woodland habitat, the group size and defense strategy of Gombe red colobus, and the hunting strategy of the Gombe chimpanzees yield very different association dynamics between red colobus and guenons. Red colobus at Gombe live in much smaller groups (12–26 individuals), and adult males actively defend against hunting chimpanzees that, unlike Taï chimpanzees, do not perform coordinated, team-oriented hunts (Boesch 1994; Stanford 1995). Chimpanzees at Gombe hunt red colobus socially and vocally; red colobus can detect and respond to chimpanzees without relying on cues from sympatric guenons (Stanford 1995). Consequently, there is little advantage to be gained from interspecific comingling, so red colobus and the two guenon species at Gombe associate briefly and infrequently (Stanford 1995).

By contrast, the stealthy hunting of Taï chimpanzees means that Diana monkeys' early detection capabilities may provide red colobus with a significant advantage in terms of

avoiding chimpanzees. At the same time, the very large groups of red colobus in Taï National Park may shield Diana monkeys from aerial predators, such that Diana monkeys can expand their use of the main canopy when associated with red colobus. Our evaluation of Diana monkey behavior in and out of association with red colobus, at times when predation pressure from chimpanzees is more or less intense, suggests that these associations incur minimal costs to Diana monkeys. They tolerate the presence of red colobus, perhaps because comingling with them provides antipredator benefits in certain contexts, and because it does not seem to increase their risk of being hunted by chimpanzees. Ultimately, these analyses provide mixed support for the hypothesis that Diana monkeys change their behavior when they are most vulnerable to predation from chimpanzees: during the chimpanzees' hunting season while associated with red colobus.

Primate communities are complex, and the costs and benefits of participating in mixed-species associations differ between ecosystems, species, and even individual groups of the same species (Chapman and Chapman 1996; Gautier-Hion *et al.* 1983; Stanford 2002). Work on polyspecific associations often frames participation in terms of actively accrued benefits such as improved foraging efficiency (e.g., Cords 1990; Peres 1992; Terborgh 1990), alarm calls from associated taxa (e.g., Bshary and Noë 1997b; Gautier-Hion *et al.* 1983), or niche expansion (e.g., McGraw and Bshary 2002; Porter and Garber 2007). However, our findings emphasize that not all participants benefit equally from mixed-species groups, but suggest that as long as the costs are not prohibitive, nuclear species may tolerate the presence of other taxa.

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