

Use of an Embedded Fruit by the Nicobar Long-tailed Macaque (*Macaca fascicularis umbrosus*): I. Familiarity to Coconuts (*Cocos nucifera* L.) and Temporal Patterns of Coconut Foraging

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Abstract: Local ecological conditions on islands and their situational derivatives often lead primates with high sensorimotor intelligence to exploit embedded foods through extractive foraging. Coconuts are one such embedded resource, but covered by two protective layers—a thick fibrous husk (mesocarp) and a woody shell (endocarp)—that harden with maturity making resource extraction time-consuming and challenging. The Nicobar long-tailed macaque (*Macaca fascicularis umbrosus*) has subsisted with the coconut palm (*Cocos nucifera*) for about two millennia leading to the development of the skills needed for foraging and processing the nut. We explored how integral the nut is to the feeding ecology of the macaques by describing a gradient of its use by the macaque groups. We tested the familiarity of groups with home ranges at different distances from palm plantations, outlining (1) consumption of coconut by four classes of groups, (2) the time spent in palm clusters/plantations by two groups, (3) the phenophases of coconuts preferred by two groups, and (4) proportionate consumption of coconuts with respect to other dietary items. Two coastal groups, one in an urban landscape and the other in a forest-farm ecotone, showed higher dependence on coconuts, with strict seasonal feeding, and longer forays into palm cluster/plantations, and chose more mature coconuts than an inland group. We conclude by reporting the hourly distribution of coconut foraging across annual cycles and between the highest/lowest feeding months along with determinants of coconut consumption per foray.

Keywords: Human-macaque competition, dependence on coconut, coconut-based resource competition, coconut consumption, feeding ecology, feeding seasonality, Nicobar archipelago

Introduction

Rapid changes in primate habitats—diminution, fragmentation and degradation—due to human activities (Estrada *et al.* 2012; McKinney 2015) require commensurate behavioural changes and/or new adaptations on the part of the primates, especially for procuring food. Such behavioural adaptations range from changes in the proportional use of food items already in their diet to the opportunistic inclusion of novel items. These new adaptations, however, can be problematic (Sih *et al.* 2011), especially in the uptake of resources shared with humans, when they can result, as such, in competition and conflict. The study of behavioural flexibility in these circumstances is not only important to understand the primate's adaptive capacities, but also has implications for managing human – non-human primate coexistence (McLennan *et al.* 2017). Sih (2013) provided a framework called HIREC (human-induced rapid environmental change) to understand species-specific selection pressures and dietary flexibilities,

and adaptive potential and, thus, overall phenotypic flexibility in response to artificial transformation of environments and ecosystems.

The Nicobar long-tailed macaque *Macaca fascicularis umbrosus* (Miller, 1902), one of 10 subspecies of *M. fascicularis* (see Fooden 1995), is believed to have dispersed to the Nicobar group of the Andaman and Nicobar Islands in the Indian Ocean *c.* 1.7–0.6 Ma (Brandon-Jones 1998; Fooden 2006; Smith *et al.* 2007; Liedigk *et al.* 2015). As island dwellers these monkeys provide for an interesting case study with regard to the development of new feeding habits and how a closed population copes with changes resulting from human activities and the resulting depredation of their habitats. They occur on three islands—Great Nicobar, Little Nicobar and Katchal—in the maritime boundary of India (Umapathy *et al.* 2003). One of the most ubiquitous tropical palm species, the coconut (*Cocos nucifera*) in its domesticated form, colonized the islands *c.* 2,250–2,500 years ago, possibly with the arrival of humans from Southeast Asia (see Gunn *et al.* 2011;

Niral and Jerard 2018). The macaques on the islands have co-existed with the coconut palm for *c.* 2 millennia, allowing for their familiarization with the palm and its fruit. It is to be noted, however, that a long period of co-occurrence between the macaque and the coconut palm does not necessarily imply the emergence of a consumer-food association uniformly across the island ecosystems the macaques occupy—the coconut palm is coastal and the macaques are not strictly coastal-dwelling (Umapathy *et al.* 2003; Velankar *et al.* 2016; Rajeshkumar *et al.* 2017). As such, the coastal-dwelling groups of long-tailed macaques have been exposed to the palm, a perennial cultivar/crop, earlier and for longer than the inland/forest-dwelling groups. Such sustained exposure to the coconut palm alongside other facilitatory factors would have led to the incorporation of its fruit, the nut, into the diet of the Nicobar long-tailed macaque, similar to the case of acceptance and consumption of novel food in rehabilitated orangutans after repeated exposure and sociality (Hardus *et al.* 2015). The dietary inclusion of the coconut, unlike that of a simple fruit, is intriguing since the nutritive/edible portion of the nut is deeply embedded in tough casings—a thick fibrous husk (mesocarp) and a woody shell (endocarp)—and extracting it is not a trivial task. In addition, the challenge of extracting the kernel progressively compounds as the shell and husk get harder and more fibrous/drier, respectively, with maturity (Niral and Jerard 2018). The requisite cognitive reasoning, hierarchical decision-making and manual dexterity necessary for coconut foraging (i.e. selection of suitable palm and nut) and nut processing could not have arisen spontaneously but would have possibly been optimized gradually over generations, similar to the hierarchical processing of prickly pear cactus by long-tailed macaques in Thailand (Tan *et al.* 2016). The processing of this complex nut embedded in protective matrices further necessitates enquiry into the sensory perception aiding detection and selection of the nut; development of motor actions associated with climbing, plucking, handling, dehusking and extraction of the kernel; oral processing and, ultimately, augmentation of gustatory capacity for assessing nutritive content. Coconut processing could thus, be indicative of sensorimotor intelligence (described by Parker and Gibson 1977, 1979), hierarchical organization of processing behavior, syntactical problem solving and the general cognitive ecology of the species.

The ecological conditions on the Nicobar Islands can be used as a model, especially because currently existing differences between habitat types provide quasi-experimental conditions for the investigation of the development of (new) foraging techniques under the conditions of the HIREC framework. We aimed to study how the macaques cope with feeding challenges in a changing ecology. We established four classes of macaque groups contingent on the habitat where they live and their access to and consumption of coconuts: (1) far from palm plantations/clusters, with no exposure to or dependency on coconuts; (2) semi-urban; (3) largely in closed, inland forest, but with limited access to coconuts; and (4) in a coastal forest and coconut plantation ecotone or mosaic. Based on our preliminary observations and pilot studies, we developed four

parameters to enunciate the extent of coconut consumption: (1) number of coconuts consumed by a group; (2) time spent by a group in a coconut plantation; (3) proportionate feeding on coconut with respect to other food items; and (4) ratio of immature/mature coconuts eaten. We expected groups with access to plantations to use more mature coconuts, requiring sophisticated processing skills but providing more nutrition. We also recorded the daily pattern of coconut foraging in two temporal contexts: (1) between annual cycles; and (2) between the months when coconut-feeding was highest and lowest. Due to the disparity in feeding quantities, hourly distribution of coconut foraging was hypothesized to differ between the highest and the lowest feeding months. Finally, we anticipated that both time spent in palm plantations and strength of feeding individuals would have a quadratic relationship with coconut consumption characterized by positive influences at lower values and negative influences at higher values.

Methods

Study site

The study was conducted on the islands of Great Nicobar and Katchal in the Nicobar archipelago lying between 93°38'05.6" and 93°57'13.7"E and 6°44'7.8" and 7°13'46.6"N, and between 93°28'32.9" and 93°18'06.8"E and 7°52'24.2" and 8°1'33.6"N, respectively. The two major forest types in these islands are the Andaman tropical evergreen forest and the Andaman semi-evergreen forest (India State of Forest Report 2019). The islands have a high degree of floral (14%) and faunal endemism (Nayar and Shastry 1987; Balakrishnan 1989; Rao 1989). The major vegetation types in the archipelago include littoral beach formations, mangroves, lowland swamps of *Pandanus* and *Barringtonia*, and inland, wet, evergreen vegetation (Hajra *et al.* 1999; Arora 2018). The islets also have plantations of coconut palm, red oil palm and other species introduced for commercial crops or for ornamental value. Fishing and coconut and areca-nut cultivation constitute the major livelihoods of the settlers, although many have recently taken up government service or have started private businesses (Arora 2018).

Study Groups

We chose four categories of long-tailed macaque groups for the study. Category-1 included three groups from Great Nicobar that did not range in coconut plantations and, hence, were expected to not consume coconuts. These groups were located progressively farther away from plantations with the first, second and third at 670 m, at 1.9 km and at 2.6 km, respectively, from coconut palm plantations. They were characterized as “forest dwelling”. The Temple Run (TR) group in Category-2 accessed the semi-urban landscape of the town of Campbell Bay on Great Nicobar (Table 1). The habitat used by TR was interspersed with human habitations, home fruit/vegetable gardens, government offices, mechanical workshops, temples, markets, roadways, waste dumps and patches of vegetation at various stages of degradation. It was,

hence, characterized as “coastal and urban-dwelling”. The Forest Camp (FC) group in Category-3 ranged primarily in the relatively undisturbed forest of Katchal and in a single coconut plantation that had begun fruiting in 2014. We designated FC as “forest and plantation dwelling”. Category-4 included the Baywatch (BW) group that ranged in an agricultural-forest ecotone comprising mixed evergreen forest and patchily distributed coconut plantations in the coastal region of Katchal. BW was characterized as “coastal forest and plantation dwelling.”

Field methods

We began by exploring the familiarity of the three Category-1, forest-dwelling groups with early (P2) and matured phenophases (P6) of coconuts against positive controls. The experiment involved (1) placing one or two coconut(s) of either P2 or P6 stage on the path of the target group at a distance of 20–25 m in full view followed by (2) returning to the experimental spot after 3–4 days to record the displacement/fate of the coconut(s). Before conducting the aforementioned experiments, we performed control trials using native fruits growing within the range of the group. To maximize the possibility of engaging with the fruits, we presented them almost at the end of their respective fruiting seasons so ensuring that trees within visible range had minimal fruits. Experiments were conducted in the early evening when foraging activities remain high and groups are nearing their sleeping sites. Since there are other fruit-eaters such as rodents, shrews and pigeons, we placed a few fruits off the path of the groups for validating that the intended fruits were eaten by monkeys alone. We used fruit of the fig, *Ficus auriculata* for the farthest group, fruit of *Spondias pinnata* for the intermediate group, and fruit of *Calamus dilirectus* for the group closest to coconut palm plantation. We drew our inferences based on the reasoning that in scenario (1) of the displacement of the coconut that physical engagement with the nut was certain

and indicative of partial familiarity, whereas, in the scenario (2) of no displacement, physical contact was avoided due to neophobia and/or indifference and hence, indicative of unfamiliarity with the nut. We conducted two trials for every coconut phenophase-group pairs. Since, the location of experiments had agents (e.g., wild boar and indigenous tribes) that could interfere with the experiments, i.e. displace the coconut, we combed the location for secondary signs of those agents. If this yielded interference, we repeated the trial. We maintained an inter-trial interval of 1–2 month(s).

The demography of the three groups of the remaining three categories from the beginning till the end of the study is shown in Table 1. Since the BW and TR groups were part of previous behavioral research, we just habituated the group to the altered field team from November, 2017 to February, 2018. We failed to habituate the FC group, despite a year-long attempt, and, as a result, it was studied using a different field protocol. Although BW was habituated, following the group into natural vegetation was hindered by thick undergrowth of cane, bamboo and shrubs. We were, therefore, unable to establish a comprehensive description of the general feeding ecology of the group. Because FC was not habituated, enumeration of the coconuts they fed/plucked was done by scanning the plantation after their departure. Lack of habituation of FC also led to inaccurate estimates of the monthly demography of the group. We, therefore, recorded (1) plucking/feeding of fresh coconuts with corresponding time and the identity of the individual (whenever possible), (2) duration of time spent in the coconut plantation/cluster, and (3) the phenophase of the coconut fed on for one or another pair of focal groups, to study their ecological dependence on coconuts.

To compare coconuts fed between BW and TR, we computed *per capita* consumption. On similar lines, we computed *per capita* duration of time spent by BW and TR in a day in coconut plantation/clusters. Based on our reasoning that groups newly introduced to coconut (as a food resource)

Table 1. Habitat classifications, locations and demographic structure of the three groups within Category-2, Category-3 and Category-4 included in the study from January 2018 to February 2020. Effective troop size combines individuals >2 years of age.

| Troop Identity | Habitat Category | Location | Demography | | Effective troop size (range) |
|----------------|---------------------------|---------------|---|--|------------------------------|
| | | | Jan, 2018 | Feb, 2020 | |
| Temple Run | Urban/Home garden | Great Nicobar | Adult ♂ - 1 Adult ♀ - 5 Juvenile ♂ - 7 Juvenile ♀ - 2 Infants - 2 | Adult ♂ - 1 Adult ♀ - 4 Sub-Adult ♂ - 3 Juvenile ♂ - 3 Juvenile ♀ - 4 Infants - 3 | 12-12 |
| Baywatch | Coastal Forest/Plantation | Katchal | Adult ♂ - 2 Adult ♀ - 12 Juvenile ♂ - 8 Juvenile ♀ - 4 Infants - 2 | Adult ♂ - 5 Adult ♀ - 13 Sub-Adult ♂ - 1 Juvenile ♂ - 9 Juvenile ♀ - 9 Infants - 9 | 21-28 |
| Forest Camp | Inland Forest | Katchal | Adult ♂ - 4 Adult ♀ - 19 Sub-Adult ♂ - 4 Juvenile ♂ - 16 Juvenile ♀ - 11 Infants - 8 | Adult ♂ - 5 Adult ♀ - 20 Sub-Adult ♂ - 3 Juvenile ♂ - 20 Juvenile ♀ - 14 Infants - 11 | 52-62 |

Table 2. Characterization of different phenophases of coconut and their identifying features.

| Developmental Phase | Characteristics | Indicators for identification |
|---------------------|--|---|
| P1 | Full size/volume not attained | Kernel absent; husk is soft, color of coconut color is bright |
| P2 | Full size/volume attained but kernel formation has not begun | Thin and transparent (jelly-like) kernel |
| P3 | Kernel is soft, dense and whitish and is yet to cover upper wall of endosperm | Relatively soft shell; kernel absent at the top wall of the endosperm |
| P4 | Kernel at the lower hemisphere is harder and thicker than P3 but soft at the upper wall of the endosperm | Hard shell at the lower hemisphere but soft beyond it; jelly-like kernel on the top wall of the endosperm |
| P5 | Shell at the top hemisphere has almost thickened but not fully and the kernel on the top wall has hardened | Hard shell beyond the lower hemisphere; thick and white kernel at the top wall of the endosperm |
| P6 | Sound of coconut water is heard when coconut is rocked | Extremely hard exocarp, extremely hard shell, and very thick and dense kernel |

would feed on early phenophases of coconut relative to groups with early/prolonged exposure, we recorded the phenophases of coconuts fed by FC and by BW from January to October, 2019. We first characterized phenophase into six stages based on volume, shell lignification and kernel extent/density (following fruit development indicators suggested by Rapoport *et al.* [2013] for stone/drupe fruits) and secondly, screened all freshly plucked/fed coconuts during observations to record phenophase. Detailed characteristics and physical identifiers of the six phenophases of coconut are shown in Table 2. Coconut foraging was characterized by events of plucking the fruit, acquiring dislodged fruits and feeding directly on them. In the context of coconut feeding, we defined “processing” as the act of removal of the inedible portion of the nut (i.e. husk/fibre) culminating in perforation of the shell. As a corollary, a coconut from which the liquid endosperm and/or the kernel is/are gathered is “processed,” a coconut with the husk incompletely removed is “partially processed,” and the coconut that has been plucked and/or handled, but not manipulated is “unprocessed”. Field methodologies specific to the groups are described below.

Temple Run and Baywatch groups

We followed TR from March, 2018 to February, 2020 and BW from March, 2018 to October 2019. Groups were followed from dawn to dusk at least once a week and a minimum of five days in a month. Besides determining the phenophase of the coconuts, we recorded coconut plucking/feeding and their associated variables (such as time of day and the fate of the coconut handled), and the time spent in the coconut plantation or cluster (thinly distributed coconut palms). We also noted the general feeding ecology of the group using an “all-occurrences” behavioral sampling framework with each session lasting for 10 minutes. We classified food items based on their origin into plant-derived foods (such as fruits and seeds/nuts), animal-derived foods (such as eggs and insects), artificial/synthetic foods (such as fruit juice and biscuits) and coconuts, demarcated as fresh (≤ 3 days post-detachment from

the palm), putrid (>3 days post-detachment from palm), and scavenged (processed coconuts that are partially eaten and/or discarded by monkeys or people). During an all-occurrences session, we ascribed an “event” to an instance of feeding by an individual; an additional event was allotted to the same individual within the all-occurrences session if feeding terminated for at least one minute and/or if the food item changed; alternatively, if feeding spilled over to the following all-occurrence session, an additional event was recorded. Demography of the group along with “effective group size” (individuals above two years of age) was monitored on a monthly basis.

Forest Camp group

During the process of habituation of the FC group (from May to December 2017), we determined the range of FC and ascertained that the group accessed a single coconut plantation of 5 ha. However, the group used about 28% of the plantation. As a consequence, coconuts that had been fed on by the group could be recorded just by combing the coconut plantation. A team of 2-4 field personnel scanned the plantation for fed and unfed coconuts once every week and for a minimum of five days in a month beginning in March, 2018 and ending in October, 2019. We maintained a coconut-detection rate of $\geq 96\%$ and recorded the phenophases of every coconut found. We failed to record the time the group spent in the coconut plantation and the effective group size systematically because of the constraints previously mentioned.

Data analysis

The category, “coconuts plucked” was an absolute count of coconuts procured directly from the palm, and “coconuts consumed” maintained count of coconuts the monkeys fed on, which included those that are dislodged and/or acquired directly from palms. We sampled TR for a period of 24 months, and BW and FC for 20 months, the latter two of which began in March, 2018. To aide comparison of coconut consumption between TR and BW, we determined *per capita* consumption by dividing absolute daily consumption with

effective group size. The effective group size was calculated monthly and included individuals that could potentially feed on coconuts, i.e. those >2 years of age (Das *et al.*, in prep.).

We took two broad statistical approaches to (1) contrast patterns of coconuts plucked/fed between groups by modeling absolute coconut consumption during every sampling day within a generalized linear model (GLM) and monthly coconuts plucked/fed within a generalized least square model (GLS), and to (2) detect monthly trends in absolute coconuts plucked/fed (of an individual group) by employing One-way ANOVA followed by *post-hoc* paired comparisons. We excluded the FC group from the GLM and the GLS analyses since the effective group size could not be determined on a monthly basis.

Similarly, we derived a *per capita* figure for the “time spent in coconut cluster” in a day, and presented it as a monthly figure for comparisons within and between the two groups, TR and BW. As a consequence of range shifting by TR during the study period, we moved from delineating a coconut patch during March–November, 2018 (Phase-1) to demarcating a coconut cluster and/or individual coconut palms during December, 2018 to February, 2020 (Phase-2).

Taking advantage of the GLM approach in RStudio v.1.2.5033 (RStudio Team 2020), we used the “predict()” function to project average monthly feeding/plucking of coconuts by BW and by FC, and monthly duration of time spent in coconut plantations by BW during November, 2019 to February, 2020, to discern periodicity. We used coconut consumption data of TR and BW from March, 2018 to February, 2020 and from March, 2018 to October, 2019, respectively to predict values of the missing months. Applying the same approach, we estimated average monthly duration of time spent in the coconut plantations during November, 2019 to February, 2020 by BW using monthly values of TR from December, 2018 to February, 2020 and monthly values of BW from November, 2018 to October, 2019.

In order to test seasonality in coconut feeding, coconut plucking and duration of time spent in palm cluster/plantation of TR and BW across the two years of the study, we regressed the data onto the standard equation for seasonal cycle, $y = \alpha + \beta \sin(2\pi t) + \gamma \cos(2\pi t) + \varepsilon$ (Equation 1) and checked for fit.

We also studied hourly pattern of coconut foraging across the day using GLS models. We divided daily activity period of the groups into time intervals of half an hour beginning at 05:01:00 h and ending at 18:00:00 h (No. of time slots = 26) followed by tabulation of the foraging activities involving the coconut over all the sampled days in the first and the second coconut feeding cycles. The first and the second annual coconut feeding cycles began in March, 2018 and continued till February, 2019 and from March, 2019 till February, 2020, respectively.

We compared the hourly profile of coconut foraging of the two groups independently between periods of the highest (August–September) and the lowest (April–May) coconut consumption by combining incidences of coconut foraging made during the two feeding periods from the two years to

generate a consolidated hourly profile for each group. To study the exact difference in coconut foraging across individual time slots between the two feeding periods, we used paired tests and for comparison within periods, we used parametric or non-parametric ANOVA.

Finally, to study the relationship between time spent in coconut plantations/clusters and the number of unique individuals feeding on coconuts with the absolute number of coconuts consumed during a visit to the coconut cluster/plantation, we undertook nonlinear regression analyses. The number of coconuts consumed during a foray into the cluster/plantation was maintained as a dependent variable and either duration of stay or number of unique feeding individuals was individually considered as the independent variable. In the case of TR, time spent in the coconut plantations was considered from only Phase-2. Analyses for BW considered data collected during whole-day sampling and non-whole day sampling through the 20 months of observation.

Ethical note

The study was exclusively observational. The sole field-based behavioral experiment received approval from the Institutional Animal Ethics Committee of the University of Mysore and complied with the 2014 Code of Best Practices for Field Primatology of the International Primatological Society and the American Society of Primatologists.

Results and Interpretations

The experiment probing familiarity of coconuts in groups of Category-1 showed that the two groups farthest from the coconut plantations were completely unfamiliar with the coconut since coconuts across the eight trials were found intact and in place even though most fruits planted on the group’s route were consumed (almost none off the route) (Supplementary Table S1). In the case of the group closest to a coconut plantation, however, we found a P6 coconut displaced by 7 m and one of the three pores tampered with in the first trial. The tampering pattern of the coconut was consistent with processing attempts by monkeys familiar with coconuts. Despite the one positive trial, three other trials generated negative results and we inferred partial familiarity with coconut by the group. A trial involving a P2 coconut was repeated with the farthest group since both coconuts were removed by people (trampled grass was detected around the spot) during the first trial.

The remaining study groups familiar with coconuts followed very specific routes to enter and exit palm plantations, and did so when the plantations were not guarded. Heightened vigilance and alertness were observed in the form of rapid bursts of terrestrial locomotion, slow arboreal movements on palm canopies, raised tail, erect shoulder hair, pointed body posture, extreme sensitivity to sounds and heightened reactivity when groups accessed regions of frequent/past encounters with people and dogs. Often, nuts obtained from such risky locations were transported to safe places and dense vegetation adjacent to the plantations. Typically, subordinate, old

Table 3. Results of generalized linear model of daily coconut consumption using group identity (Temple Run and Baywatch), effective troop size and months as predictors.

| Daily coconut consumption($\text{Ind}^{-1} \text{Day}^{-1}$) ~ Troops + Months + Effective troop size | | | | |
|---|----------|-------|---------|---------|
| Coefficients | Estimate | SE | Z | p |
| <i>Intercept</i> | 2.628 | 0.178 | 14.752 | <0.0001 |
| <i>Temple Run</i> | -0.941 | 0.089 | -10.522 | <0.0001 |
| <i>Effective group size</i> | 0.039 | 0.007 | 5.707 | <0.0001 |
| January | 0.235 | 0.061 | 3.865 | <0.0001 |
| February | 0.446 | 0.058 | 7.704 | <0.0001 |
| March | 0.080 | 0.055 | 1.463 | 0.1435 |
| May | -0.270 | 0.058 | -4.687 | <0.0001 |
| June | 0.138 | 0.053 | 2.584 | 0.0098 |
| July | 0.546 | 0.050 | 10.898 | <0.0001 |
| August | 0.808 | 0.048 | 16.689 | <0.0001 |
| September | 0.575 | 0.050 | 11.459 | <0.0001 |
| October | 0.444 | 0.051 | 8.706 | <0.0001 |
| November | 0.500 | 0.059 | 8.421 | <0.0001 |
| December | 0.363 | 0.058 | 6.213 | <0.0001 |

*Baywatch is the control troop; April is the control month

Table 4. Results of the generalized least square modeling of monthly coconut consumption using annual cycle, month and troop identity (Temple Run (TR) and Baywatch (BW)) as predictors. The summaries of the best three models are shown below. The models have been fitted by using the restricted maximum likelihood method (REML).

| Monthly coconut consumption($\text{Ind}^{-1} \text{Day}^{-1}$) ~ Annual cycle + Month + Troop | | | | | | | | |
|---|-------|----|--------|---------------------|----------|------|-------|---------|
| Correlation structure | AIC | df | ϕ | Coefficients | Estimate | SE | t | P |
| AR(1) | 88.33 | 48 | 0.40 | <i>Intercept</i> | 3.22 | 0.54 | 5.95 | <0.0001 |
| | | | | <i>Annual cycle</i> | -0.12 | 0.21 | -0.58 | 0.57 |
| | | | | <i>Month</i> | 0.05 | 0.03 | 1.92 | 0.06 |
| | | | | <i>TR</i> | -1.21 | 0.23 | -5.24 | <0.0001 |
| AR(1 Troop) | 88.31 | 48 | 0.40 | <i>Intercept</i> | 3.22 | 0.54 | 5.92 | <0.0001 |
| | | | | <i>Annual cycle</i> | -0.12 | 0.22 | -0.57 | 0.57 |
| | | | | <i>Month</i> | 0.05 | 0.03 | 1.81 | 0.08 |
| | | | | <i>TR</i> | -1.20 | 0.24 | -5.09 | <0.0001 |
| AR(1 Month) | 86.87 | 48 | 0.46 | <i>Intercept</i> | 3.19 | 0.38 | 8.41 | <0.0001 |
| | | | | <i>Annual cycle</i> | -0.10 | 0.10 | -0.95 | 0.35 |
| | | | | <i>Month</i> | 0.04 | 0.03 | 1.45 | 0.15 |
| | | | | <i>TR</i> | -1.19 | 0.15 | -7.94 | <0.0001 |

Table 5. Summary of fitting seasonal cyclicality to “monthly coconut consumption (MC)”, “monthly coconut plucked (MP)” and “duration of time spent in coconut cluster/plantation (MD)” of Temple Run (TR) and Baywatch (BW) using the equation $y = \alpha + \beta \sin(2\pi t) + \gamma \cos(2\pi t) + \varepsilon$.

| Variable | Troop | F (df1,df2) | p_F | R ² | Co-efficient | Estimate | SE | t | p |
|----------|-------|-------------|--------|----------------|--------------|----------|------|-------|--------|
| MC | TR | 10.0 (2,21) | <0.001 | 0.53 | α | 0.96 | 0.05 | 18.98 | <0.001 |
| | | | | | β | -0.18 | 0.07 | -2.45 | 0.023 |
| | | | | | γ | -0.27 | 0.07 | -3.75 | 0.001 |
| MP | TR | 11.8 (2,21) | <0.001 | 0.53 | α | 1.00 | 0.06 | 17.20 | <0.001 |
| | | | | | β | -0.27 | 0.08 | -3.33 | 0.003 |
| | | | | | γ | -0.29 | 0.08 | -3.52 | 0.002 |
| MC | BW | 5.94 (2,21) | 0.009 | 0.36 | α | 2.16 | 0.12 | 18.18 | <0.001 |
| | | | | | β | -0.41 | 0.17 | -2.47 | 0.022 |
| | | | | | γ | -0.40 | 0.17 | -2.40 | 0.025 |
| MP | BW | 7.18 (2,21) | 0.004 | 0.41 | α | 2.26 | 0.12 | 19.35 | <0.001 |
| | | | | | β | -0.44 | 0.16 | -2.69 | 0.013 |
| | | | | | γ | -0.44 | 0.16 | -2.67 | 0.014 |
| MD | TR | 4.29 (2,12) | 0.040 | 0.42 | α | 3.13 | 0.28 | 11.39 | <0.001 |
| | | | | | β | 0.56 | 0.38 | 1.48 | 0.16 |
| | | | | | γ | 0.94 | 0.40 | 2.39 | 0.03 |
| MD | BW | 5.45 (2,21) | 0.01 | 0.34 | α | 10.66 | 0.79 | 13.57 | <0.001 |
| | | | | | β | -3.44 | 1.11 | -3.10 | 0.005 |
| | | | | | γ | -1.28 | 1.11 | -1.51 | 0.26 |

(>10 years), experienced and late juvenile (σ : 3–4.5 years; ϕ : 3–6 years) individuals entered plantations about twice a day either alone or in groups of 2–3, followed by dominant and younger individuals. Groups spent between 6% and 33% of their activity period in palm plantations. Females with infants (<1 year) were the last individuals to enter plantations and avoided areas that were heavily guarded, although they often “parked” their infants communally with a single mother and/or with an older offspring at safer natural locations when they foraged on coconuts. Regardless, parties foraging for coconuts reached a maximum of five individuals, and entries into plantations occurred in phases, with individuals selecting palms in and around the same cluster as that of experienced individuals from previous foraging parties and exited after feeding on an average of 1.59 nuts/ind.

During the study, the observable ranging of the Category-2 group TR drastically shifted and contracted in response to a combination of factors, which included inter-group conflict, human provisioning of fruits and vegetables, clearing of natural refuges, open dumping of domestic food waste and the construction of houses. The coastal ranging and plantation use of BW was equivalently altered by the presence of four indigenous households who secured their horticulture plantations against monkeys either with catapults and/or by employing guard dogs. However, despite active hindrances by humans to coconut feeding by TR during 22% of the sampling days ($N_{\text{Interferences/TR}} = 36$ days) and interventions by both, humans and guard dogs in the case of the Category-4 group, BW on 27% of sampling days ($N_{\text{Interferences/BW}} = 40$ days), the “number of coconuts consumed (#Coconut)” and “duration of time spent in coconut plantation (Dur)” by both of the groups remained unaffected (Independent samples Wald Wolfowitz Runs test; $p_{\#Coconut/TR} = 0.96$, $p_{\#Coconut/BW} = 0.78$; $p_{\text{Dur/TR}} = 0.51$,

$p_{\text{Dur/TR}} = 0.38$). We failed to record phenophase of coconuts consumed by TR, since many coconut clusters were either within fenced compounds, in submerged regions or surrounded by inaccessible secondary vegetation. Although the ranging of TR was tracked through the day, recording their activities was at times obstructed by dense foliage and boundary walls and fences.

Coconut consumption by Temple Run, Baywatch and Forest Camp and their monthly trends

One of the ways in which we studied coconut use by the long-tailed macaques was by recording *per capita* coconut consumption. Effective group size of FC and BW rose from 21 and 52 to 28 and 62 individuals, respectively, during the study period, while in TR the effective group size remained stable at 12 (Table 1). Both, TR and BW fed on coconuts on almost all sampling days ($N_{\text{Coconut/TR}}/N_{\text{Total/TR}} = 161/164$; $N_{\text{Coconut/BW}}/N_{\text{Total/BW}} = 147/148$) and ranged from 0–42 coconuts per day and 0–124 coconuts per day, respectively, with an average of $13.23 \pm 8.64_{\text{SD}}$ and $53.74 \pm 30.20_{\text{SD}}$, respectively. FC, on the other hand, fed on coconuts in only 40% of sampling days ($N_{\text{Coconut/FC}}/N_{\text{Total/FC}} = 66/163$) at an average of $7.90 \pm 15.17_{\text{SD}}$ coconuts per day, which is marginally more than half of the average coconut consumption of TR despite a group size almost four times that of TR. Although coconuts were primarily plucked from the palm, a subset of fresh coconuts was encountered in dislodged form on the palm and on the ground. Thus, “coconuts plucked” was independent of “coconuts consumed.” Likewise, a substantial number of fresh coconuts that were acquired from the palm/ground were abandoned before completion of processing and were termed “unprocessed.”

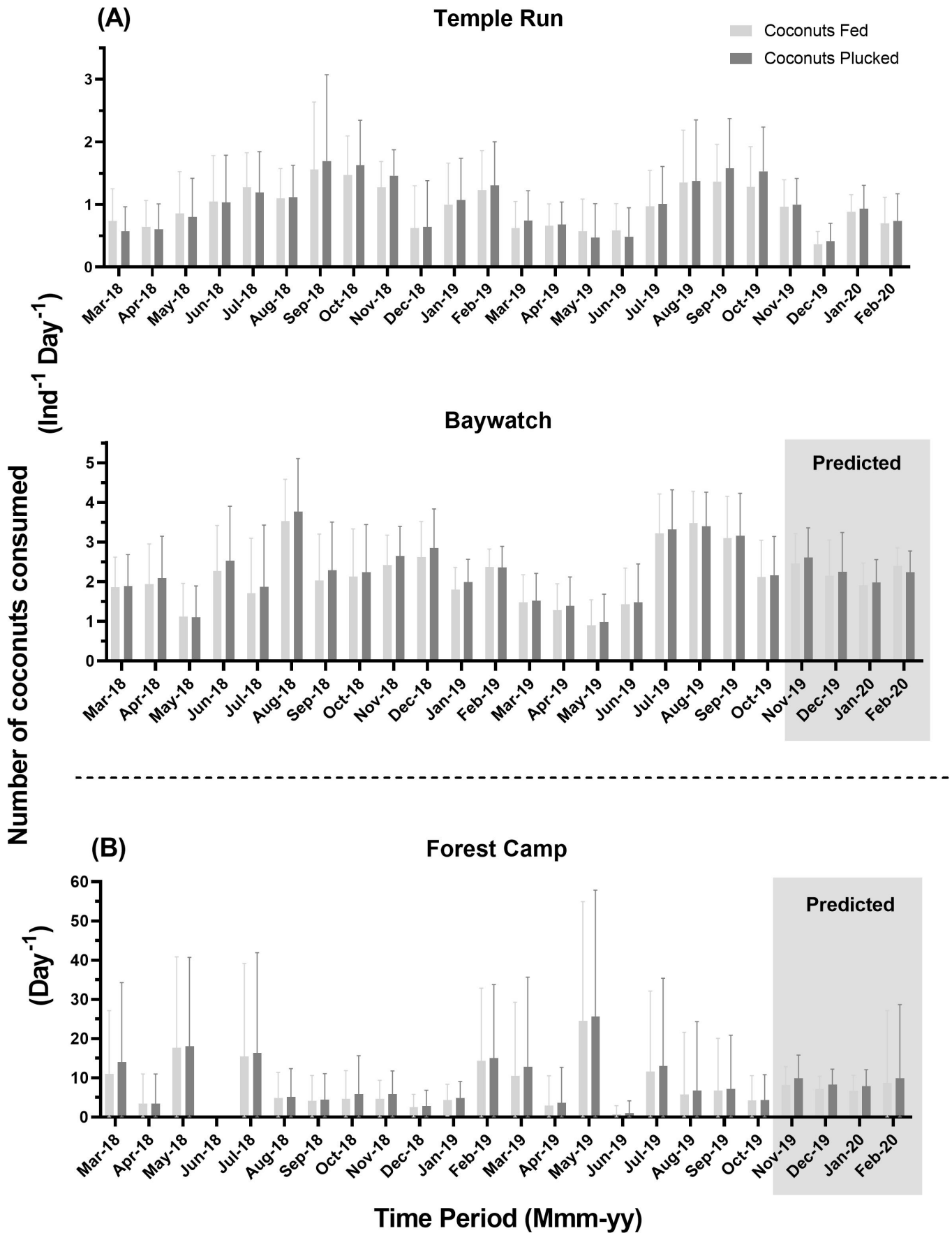


Figure 1. Monthly pattern of coconut consumption of Temple Run, Baywatch and Forest Camp groups. For ease of comparison between Temple Run and Baywatch, the unit (per individual per day) of coconut consumption is kept common. Since the unit per day of coconut consumption of Forest Camp is different from the other groups, the graph is segregated using a dotted line. The shaded area in the graph of the Baywatch and Forest Camp groups represents monthly values that were predicted using the best-fit GLM model. Note that the scales of the Y-axes are different across the three graphs.

Fresh coconuts acquired from either the palm or the ground were left unprocessed at an average of $3.15 \pm 2.51_{SD}$ coconuts per day by TR and at an average of $5.88 \pm 4.69_{SD}$ coconuts per day by BW as a result of disease, pest infestation, rodent infestation, erroneous selection and accidental dropping. Through the generalized linear model (GLM), we found (1) marginal influence of “effective group size” on coconut consumption, and (2) a higher consumption of coconuts by BW than TR across the 20 months of observation (Table 3). Results from the generalized least square model (GLS) further corroborated the difference in coconut consumption between TR and BW, despite controlling for group size. A monthly pattern of coconut consumption was not yielded in the GLS models, however, in contrast to the GLM model (Table 4). Consistent minima in coconut consumption were observed in May across the two groups, whereas the maxima differed from August in TR to September in BW, but remained stable across years ($F^{TR} = 2.19$, $p = 0.003$, $R^2 = 0.26$; $F^{BW}(19,128) = 5.41$, $p < 0.0001$, $R^2 = 0.45$; see Fig. 1). Conversely, the absolute number of coconuts plucked/fed on by the FC group remained stable across months ($KW^{FC} = 17.16$, $p = 0.58$). Both groups showed synchronized annual periodicity in plucking and feeding on coconuts across the study period (Table 5).

Duration of time spent in coconut clusters/plantations by Temple Run and Baywatch

Duration of time spent in coconut plantations by a group was used as a proxy for their coconut dependence as well as a determinant of their absolute coconut consumption in a day. The variable was measured for TR and BW but not for FC, since the group was not habituated and would flee when approached by observers. The two groups TR and BW exhibited a strong propensity to forage on coconuts despite being discouraged to do so by humans and/or dogs. The coconut foraging party of the two groups remained uniform at between one and five individuals, despite differences in group size and social structure. However, the number of individuals that entered the plantation during a foray varied between the two groups. Based on the first definition of entry and exit into a palm cluster, TR spent $251.86 \pm 157.78_{SD}$ minutes per day ($\text{Range}^{\text{Phase-1/TR}} = 0.38\text{--}10.5$ h) in coconut palm clusters during March to November 2018 (Phase-1). Following the update in the definition post-December, 2018, the daily duration of time spent in coconut plantations by TR dropped to $44.34 \pm 32.74_{SD}$ minutes per day ($\text{Range}^{\text{Phase-2/TR}} = 0.02\text{--}2.7$ h) (Phase-2). The second group, BW spent $247.9 \pm 184.90_{SD}$ minutes per day ($\text{Range}^{BW} = 0\text{--}12.18$ h) in coconut plantations despite experiencing resistance from people and guard dogs throughout the study period.

When *per capita* duration of time spent in the coconut cluster/plantation was compared between the two groups, we found that BW spent more time in coconut plantations than TR (Table 6). The shortest (*per capita*) duration of time spent in a palm cluster during the first phase (Phase-1) of the study was in March and the longest time was spent in October ($F^{\text{Phase-1/}}$

$\text{TR} = 4.46$, $p = 0.0003$, $R^2 = 0.39$). During the second phase of the study, April–May, we recorded that the shortest (*per capita*) time, and the longest (*per capita*) time in palm clusters ($KW^{\text{Phase-1/TR}} = 24.15$, $p = 0.04$) was in October. In slight contrast to TR, BW consistently spent the least (*per capita*) time in May in both years, though the highest time spent by individuals differed across the two years ($F^{BW}(19,41.05) = 11.53$, $p < 0.0001$, $R^2 = 0.44$). Finally, we found no support in favor of cyclicity of time spent in coconut palm clusters/plantations in either TR or BW (Table 5), as is apparent from the monthly patterns illustrated in Figure 2.

Phenophases of coconuts consumed by Baywatch and Forest Camp

We found that all phenophases of coconuts were consumed by both, BW and FC. The 4th and the 5th phenophases of coconuts were combined for ease of visual representation in Figure 3. P6 was excluded from the current analysis because it is not consumed when fresh by the macaques, only after putrefaction of the fibrous husk. On average, per day the FC group consumed P1 coconuts 36 times more than P4–P5 ($P1^{FC} = 6.11 \pm 1.56_{SD}$; $P4\text{--}P5^{FC} = 0.17 \pm 0.12_{SD}$), 13 times more than P3 coconuts ($P3^{FC} = 0.47 \pm 0.11_{SD}$), and five times more than P2 coconuts ($P2^{FC} = 1.34 \pm 0.25_{SD}$). Although coconuts of phenophase P1 continued to be consumed in greater proportion by BW on a monthly basis, it was nine times greater than the combined category of P4–P5 coconuts ($P1^{BW} = 25.96 \pm 17.72_{SD}$; $P4\text{--}P5^{BW} = 2.96 \pm 3.82_{SD}$), three times greater than the P3 category of coconuts ($P3^{BW} = 8.59 \pm 7.82_{SD}$) and was comparable to P2 category of coconuts ($P2^{BW} = 19.94 \pm 15.95_{SD}$). P1 and P1–P2 (i.e. combined category of P1 and P2 coconuts) showed that immature coconuts were represented in higher proportions in the records of FC than in the records of BW, in compliance with our hypothesis ($\chi^2_{P1} = 62.69$, $df = 1$, $p < 0.0001$, $\text{Prop}_{P1/FC} > \text{Prop}_{P1/BW}$; $\chi^2_{P1} = 232.05$, $df = 1$, $p < 0.0001$, $\text{Prop}_{P1-P2/FC} > \text{Prop}_{P1-P2/BW}$). Conversely, phenophases $\geq P3$ were fed on more prevalently by BW than by FC ($\chi^2_{P3} = 44.98$, $df = 1$, $p < 0.0001$, $\text{Prop}_{P3/FC} < \text{Prop}_{P3/BW}$; $\chi^2_{P4-P5} = 13.02$, $df = 1$, $p < 0.0001$, $\text{Prop}_{P4-P5/FC} < \text{Prop}_{P4-P5/BW}$). The trends of phenophases of coconuts consumed by the two groups across the 10 months of observations are shown in Figure 3.

Dietary dependence of Temple Run on coconuts relative to other food resources

We studied the feeding ecology of TR to determine the contribution of coconuts to their diet during the two annual cycles. We recorded a total of 5,864 and 8,201 feeding events during the first and the second annual cycles (AC), respectively, during which 1293 ($\text{Prop}_{\text{Coco/AC-1}} = 0.22$) events and 1385 ($\text{Prop}_{\text{Coco/AC-2}} = 0.17$) events of coconut feeding were recorded, respectively. The contribution of coconuts to all plant-based food items dropped from 32% in AC-1 to 25% in AC-2 ($\chi^2 = 59.10$, $df = 1$, $p < 0.0001$, $\text{Prop}_{\text{Coco/AC-1}} > \text{Prop}_{\text{Coco/AC-2}}$) although other plant-derived (P-D) dietary items of seeds, fruits, and tubers increased from 47% in AC-1 to 50.2% of all

Table 6. Results of generalized linear modeling of duration of visit to coconut cluster/plantation using group identity (Temple Run (TR) and Baywatch (BW)), effective group size and months as predictors.

| Duration of time spent in coconut plantation (Ind ⁻¹ Day ⁻¹) ~ Troops + Months + Effective troop size | | | | |
|--|----------|-------|--------|---------|
| Coefficients | Estimate | SE | Z | P |
| Intercept | -1.986 | 0.324 | -6.126 | <0.0001 |
| Temple Run | 1.364 | 0.161 | 8.470 | <0.0001 |
| Effective group size | 0.241 | 0.012 | 19.837 | <0.0001 |
| January | 1.503 | 0.044 | 33.959 | <0.0001 |
| February | 1.345 | 0.045 | 29.749 | <0.0001 |
| March | 0.864 | 0.049 | 17.580 | <0.0001 |
| May | -0.077 | 0.058 | -1.323 | 0.1860 |
| June | 1.076 | 0.044 | 24.198 | <0.0001 |
| July | 1.412 | 0.043 | 32.573 | <0.0001 |
| August | 1.317 | 0.046 | 28.553 | <0.0001 |
| September | 1.401 | 0.046 | 30.553 | <0.0001 |
| October | 0.908 | 0.048 | 19.097 | <0.0001 |
| November | 1.712 | 0.049 | 34.988 | <0.0001 |
| December | 1.498 | 0.045 | 33.546 | <0.0001 |

*April is considered as the control month and Baywatch is considered the control group.

Table 7. Results of the generalized least square modeling of foraging and feeding of coconuts through the day (computed in half an hour time slots) using annual cycle, time slot and group identity (Temple Run (TR) and Baywatch (BW)) as predictors. The summary of the best three models are presented below. The models have been fitted by using restricted maximum likelihood method (REML).

| Correlation structure | AIC | df | φ | Coefficients | Estimate | SE | T | p |
|---|---------|-----|------|-----------------|----------|---------|--------|---------|
| Model 1 Foraging and feeding of coconuts ~ Annual cycle + Time slot + Group | | | | | | | | |
| AR(1) | 368.96 | 104 | 0.41 | Intercept | -195.46 | 808.58 | -0.24 | 0.81 |
| | | | | Annual cycle | 0.10 | 0.40 | 0.25 | 0.80 |
| | | | | Time slot | 0.001 | 0.008 | 1.27 | 0.21 |
| | | | | TR | -3.05 | 0.42 | -7.29 | <0.0001 |
| Model 2 Foraging and feeding of coconuts ~ Annual cycle + Group | | | | | | | | |
| AR(1) | 356.06 | 104 | 0.39 | Intercept | -113.39 | 1153.88 | -0.48 | 0.64 |
| | | | | Annual cycle | 0.06 | 0.39 | 0.15 | 0.88 |
| | | | | TR | -3.05 | 0.40 | -7.63 | <0.0001 |
| AR(1 Time) | 370.11 | 104 | 0.06 | Intercept | 153.70 | 514.08 | 0.30 | <0.0001 |
| | | | | Annual cycle | -0.07 | 0.25 | -0.29 | 0.77 |
| | | | | TR | -2.96 | 0.27 | -10.92 | <0.0001 |
| Model 1' Foraging and feeding of coconuts (Ind⁻¹) ~ Annual cycle + Troop + Annual cycle*Group | | | | | | | | |
| AR(1) | -250.77 | 104 | 0.28 | Intercept | 23.45 | 46.36 | 0.51 | 0.61 |
| | | | | Annual cycle | -0.01 | 0.02 | -0.50 | 0.62 |
| | | | | TR | -28.66 | 65.88 | -0.44 | 0.66 |
| | | | | Annual cycle*TR | 0.01 | 0.03 | 0.43 | 0.66 |
| Model 2' Foraging and feeding of coconuts (Ind⁻¹) ~ Annual cycle + Group | | | | | | | | |
| AR(1) | -257.59 | 104 | 0.27 | Intercept | 9.14 | 32.44 | 0.28 | 0.78 |
| | | | | Annual cycle | -0.004 | 0.02 | -0.27 | 0.78 |
| | | | | TR | -0.02 | 0.02 | -1.08 | 0.28 |
| AR(1 Time) | -250.31 | 104 | 0.04 | Intercept | 11.34 | 24.27 | 0.47 | 0.64 |
| | | | | Annual cycle | -0.01 | 0.01 | -0.46 | 0.65 |
| | | | | TR | -0.02 | 0.01 | -1.27 | 0.21 |

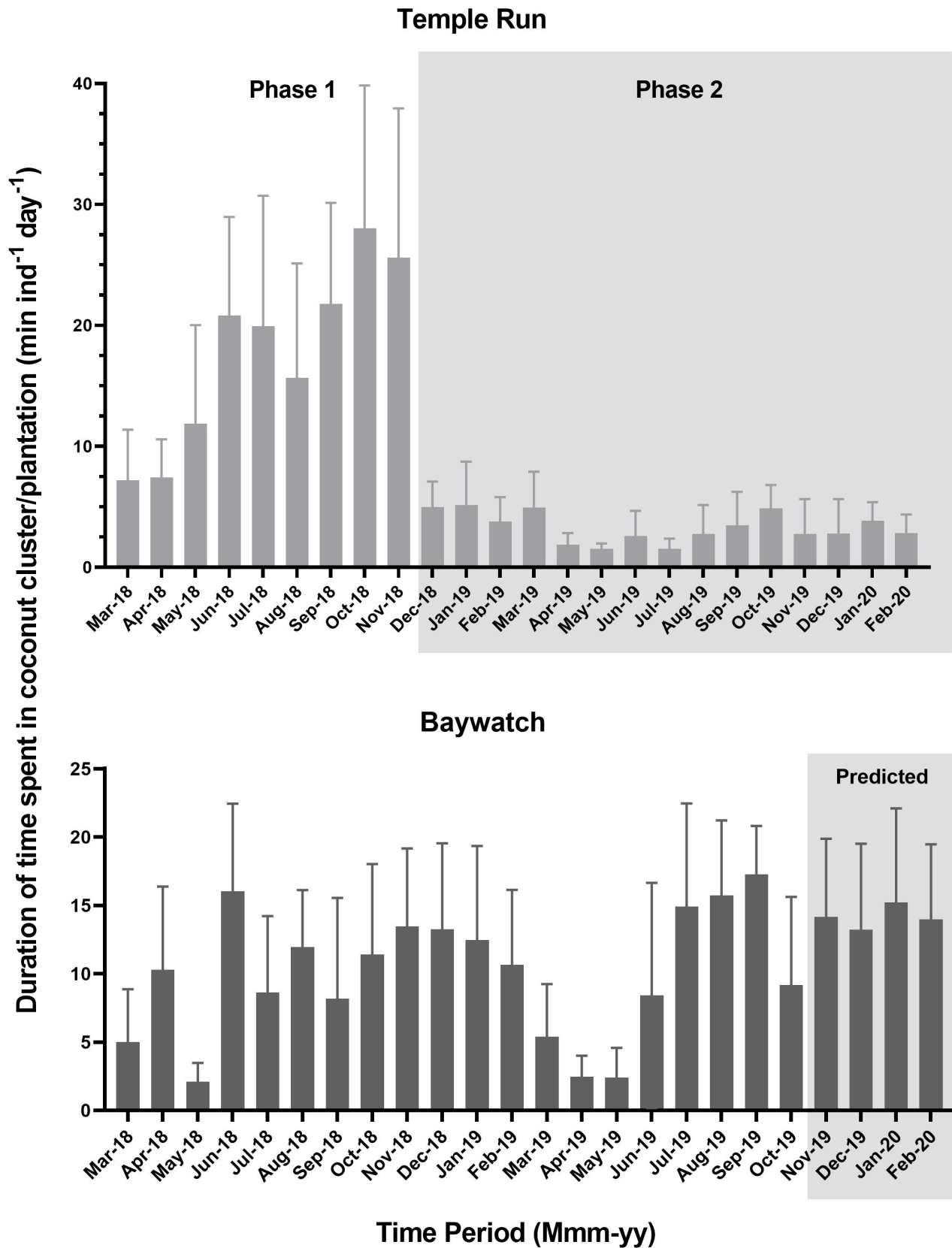


Figure 2. Monthly pattern of time spent in coconut clusters/plantations by the Temple Run and Baywatch groups. The two phases during which two different definitions of entry/exit into coconut clusters were used—Phase-1 and Phase-2—are labeled. The shaded area in the graph of Baywatch troop represents monthly values that were predicted using the best-fit GLM model. Note that the scales of the Y-axes are different across the two graphs.

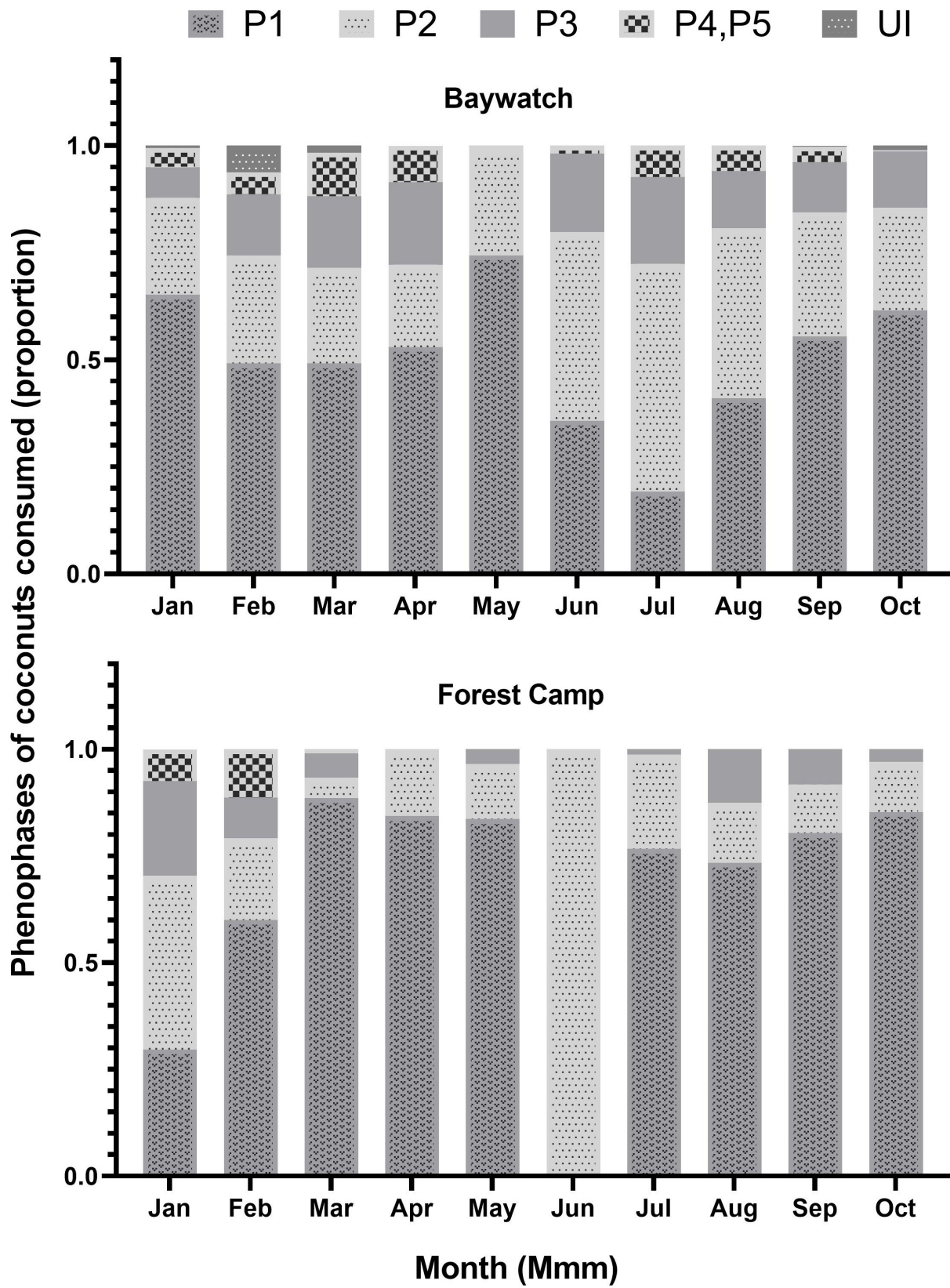


Figure 3. Monthly pattern of coconuts consumed distinguished by their phenophase in Baywatch and Forest Camp troops during January 2019 to October 2019. Each phenophase is represented in a different pattern and stacked over another during a month.

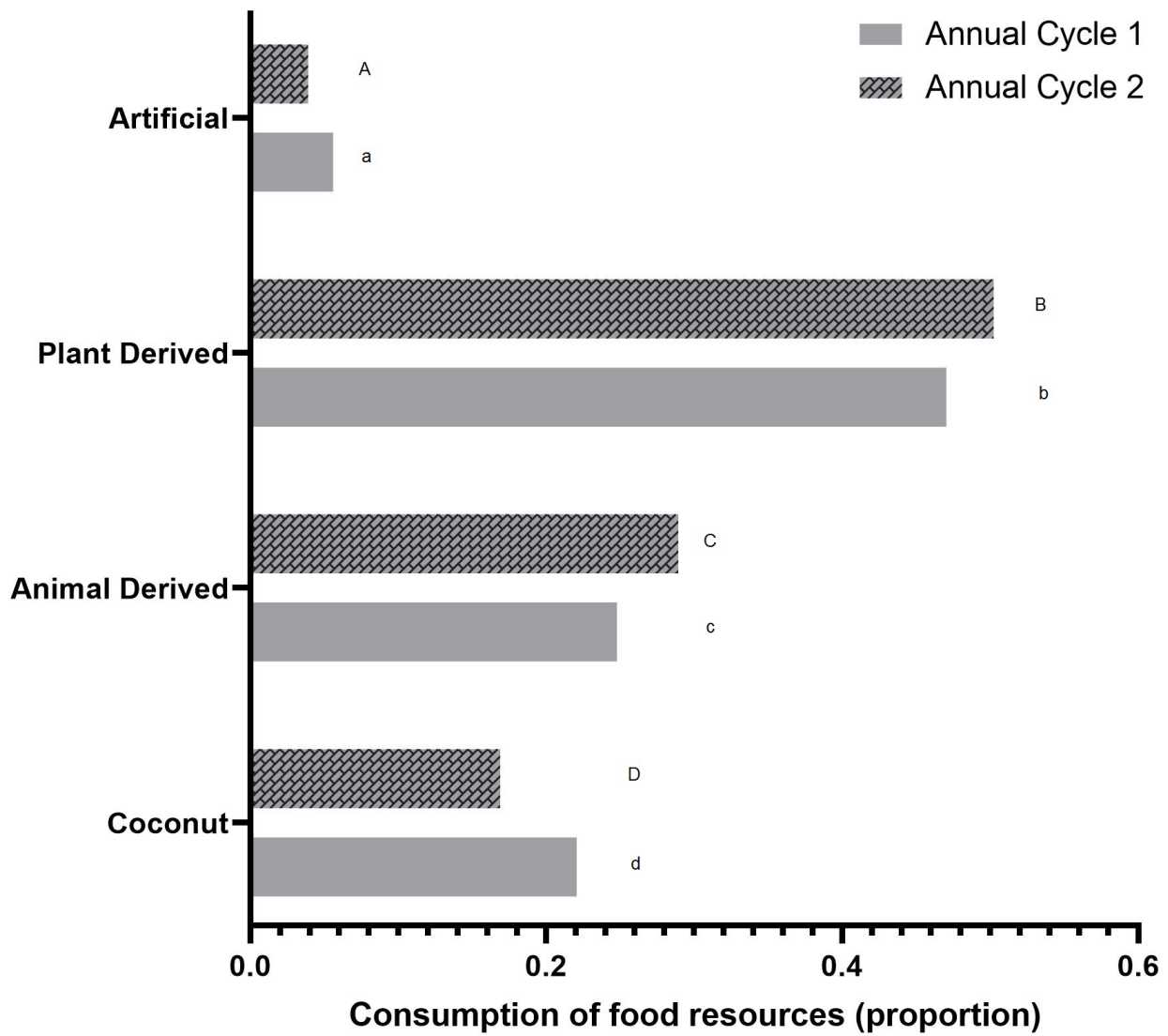


Figure 4. Comparison of the dietary allocation for different classes of food resources by the Temple Run group during Annual Cycle 1 (March 2018 to February 2019) and during Annual Cycle 2 (March 2019 to February 2020). Letters at the top of the bars denote statistical comparisons between the annual cycles and across classes of food resources within an annual cycle. Differences in the cases (upper/lower) of the letters denotes statistical differences at $p < 0.001$.

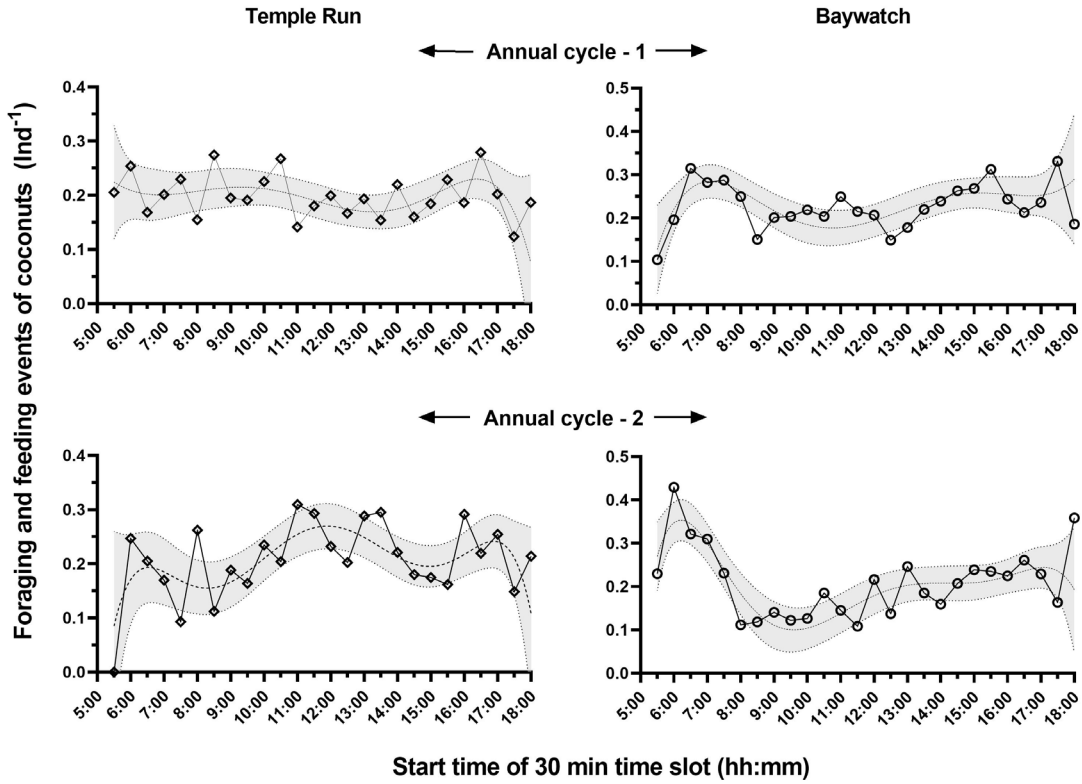


Figure 5. Temporal patterns of coconut foraging by the Temple Run and Baywatch groups during a day, averaged across an annual cycle. The two columns represent the two groups and the two rows represent the two annual cycles. The data points of the Temple Run and Baywatch groups are marked in “diamonds” and “circles,” respectively. The trends of the data are depicted using polynomial equations with area within 95% confidence intervals in shaded form, and the upper/lower bounds and mean estimates are represented as continuous curves. Note that the scales of the Y-axes are different across the graphs.

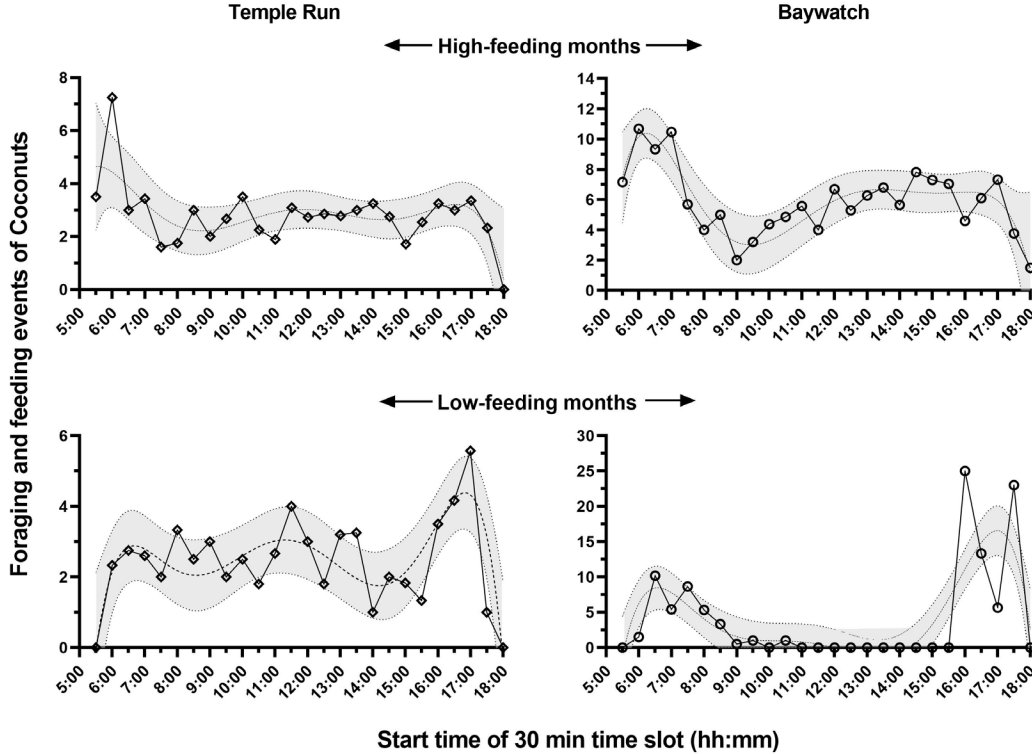


Figure 6. Temporal pattern of coconut foraging by the Temple Run and Baywatch groups during a day, averaged across the two annual cycles during the highest (August–September) and the lowest (March–April) coconut-feeding months. The two columns represent the two groups and the two rows represent the two coconut-feeding phases, i.e. highest and lowest feeding months. The data points of the Temple Run and Baywatch groups are marked in “diamonds” and “circles,” respectively. The trends of the data are depicted using polynomial equations with area within 95% confidence intervals in shaded form, and the upper/lower bounds and mean estimates represented as continuous lines. Note that the scales of the Y-axes are different across the graphs.

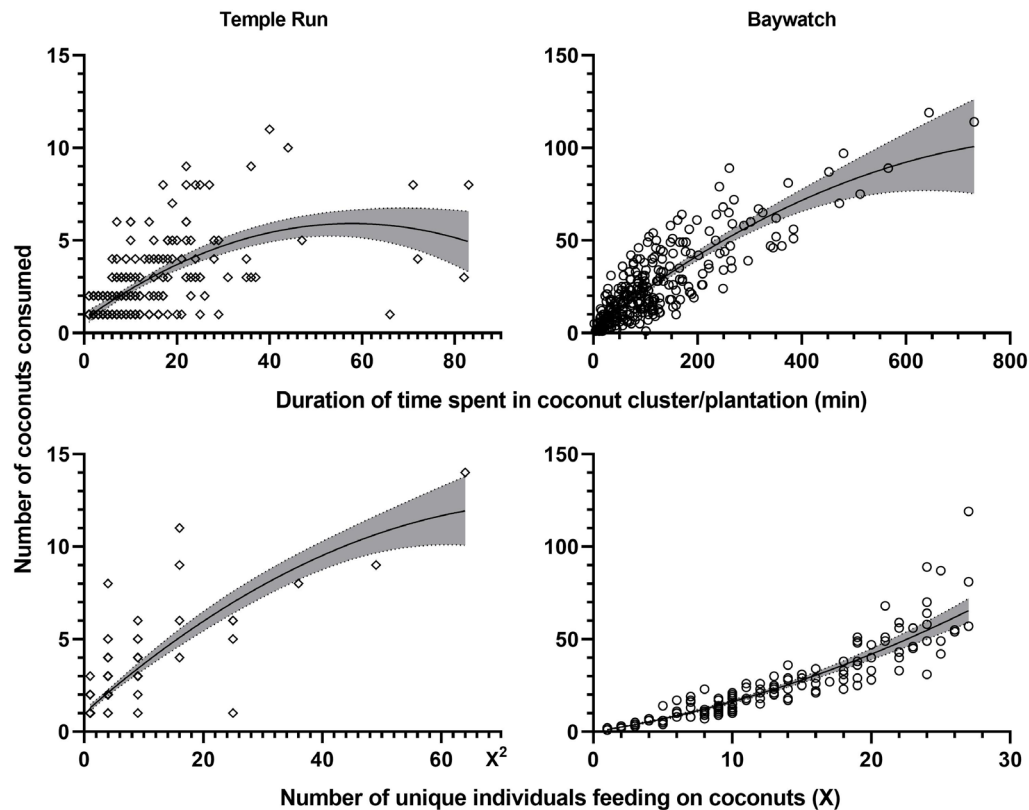


Figure 7. Relationships between coconut consumption with number of feeding individuals and with duration of time spent in coconut clusters/plantations for the Temple Run and Baywatch groups during forays. The two columns represent the two groups and the two rows represent the two covariates of coconut consumption. The data points of the Temple Run and Baywatch groups are marked in “diamonds” and “circles,” respectively. Curves depict the best non-linear regression model. Additional features in the graph include 95% confidence intervals with upper/lower bounds shown as dotted lines and the estimated regression curve a continuous line. The area between the upper and the lower bounds of the confidence interval is shaded. Note that the X-axis of the first graph in the second row (Temple Run, second variable) is squared and the scales of the axes differ across graphs (scale of the Y-axes of Temple Run is identical and scale of the Y-axes of Baywatch is identical).

feeding items in AC-2 ($\chi^2 = 13.74$, $df = 1$, $p = 0.0002$, $\text{Prop}_{D/AC-1} < \text{Prop}_{D/AC-2}$). A similar increment was noted in the dietary contributions of animal-derived (A-D) resource items (such as insects, geckos, and eggs) in the second annual year ($\chi^2 = 29.50$, $df = 1$, $p < 0.0001$, $\text{Prop}_{A-D/AC-1} < \text{Prop}_{A-D/AC-2}$) possibly as a result of a decline in the consumption of synthetically manufactured (S-M) food items (such as health drinks, fruit juice, jam, and pharmaceutical drugs) in the second annual cycle ($\chi^2 = 22.26$, $df = 1$, $p < 0.0001$, $\text{Prop}_{S-M/AC-1} > \text{Prop}_{S-M/AC-2}$) (Fig. 4). Nearly 54% of all feeding events comprised non-native food resources, including fruits (e.g., coconuts, guavas, mangos, Indian plums) seeds (e.g., casuarinas), tubers (e.g., potatoes, yams), flowers (e.g., *Peltophorum* spp., mango) and leaves (e.g., papaya).

Hourly frequency of coconut foraging by Temple Run and Baywatch across the day

The hourly frequency of coconut foraging differed between TR and BW, with BW engaging in coconut foraging twice as much, although coconut foraging of the groups remained stable across the annual cycles (Table 7). On controlling for group size, however, the difference in hourly patterns of coconut foraging between the two groups disappeared (Table 7). TR showed a uniform hourly frequency of coconut foraging through the day during both annual cycles ($\text{KW}_{\text{Cycle-1/TR}} = 22.0$, $p = 0.64$; $\text{KW}_{\text{Cycle-2/TR}} = 28.19$, $p = 0.21$) but BW

showed disproportionately lower coconut foraging during 07:31–08:00 h, 11:01–11:30 h, 12:01–12:30 h and 17:01–17:30 h in the second annual cycle ($\text{KW}_{\text{Cycle-1/BW}} = 24.47$, $p = 0.49$; $\text{KW}_{\text{Cycle-2/BW}} = 63.94$, $p < 0.0001$; Fig. 5).

We found evidence of temporal accommodation in frequency/distribution of engagements with coconuts across the day as a result of the difference in the intensity of coconut foraging during periods of the highest/lowest coconut consumption in both groups (Supplementary Table S2). Though coconut foraging of TR remained stable across time slots during the highest feeding period ($\text{KW}_{\text{High/TR}} = 14.48$, $p = 0.94$), the lowest feeding period recorded broad variations in coconut foraging throughout the day with three heightened foraging activities occurring in the morning, at pre-noon and in the early evening ($\text{KW}_{\text{Low/TR}} = 40.84$, $p = 0.02$; Fig. 6). Curiously, paired comparison of time slots between the highest consumption period and the lowest consumption period in TR showed no difference ($p^{\text{TR}} = 0.38$). BW exhibited slight variation in the first half of the day during the highest consumption period with a peak in coconut foraging in the early morning (i.e. at 05:31–06:00 h) and a trough during 08:31–09:00 h; the second half of the day registered a stable trend in coconut foraging that declined in the late evening (17:01–17:30 h) ($\text{KW}_{\text{High/BW}} = 41.40$, $p = 0.02$). The hourly profile of coconut foraging by BW was most stark during the lowest coconut feeding period wherein two isolated peaks, one in the early

morning (06:01–06:30 h) and the other during the late evening (17:01–17:30 h) were observed with almost no activity in the intervening period ($KW_{Low/BW} = 61.28$, $p < 0.0001$). In agreement with our hypothesis, paired comparison of time slots between the highest consumption period and the lowest consumption period were different ($p^{BW} = 0.02$).

Pattern of relationship between duration spent in coconut plantations/clusters and feeding individuals with coconut consumption

Considering complete forays to coconut plantations across the study period, a typical visit by TR involved an average of $1.68 \pm 1.13_{SD}$ individuals ($Range_{Foray/TR} = 1–8$ individuals) spending $12.23 \pm 12.67_{SD}$ minutes ($Range_{Duration/TR} = 1–83$ min) to feed on $2.62 \pm 2.28_{SD}$ coconuts ($Range_{Coconut/TR} = 1–14$ coconuts). In comparison, forays to plantations by BW lasted for $127.92 \pm 128.82_{SD}$ minutes ($Range_{Duration/BW} = 2–741$ min) during which $11.69 \pm 7.46_{SD}$ individuals ($Range_{Foray/BW} = 1–27$ individuals) fed on $25.07 \pm 21.12_{SD}$ coconuts ($Range_{Coconut/BW} = 1–119$ coconuts). On running the first series of regression models to identify predictors of coconut consumption, we found a quadratic association with a decreasing trend between duration spent in coconut clusters/plantations and number of coconuts consumed in both groups (Adjusted $R^2_{TR} = 0.38$, $Sy_{XTR} = 1.51$; Adjusted $R^2_{BW} = 0.67$, $Sy_{XBW} = 2.25$). The point of inflection in coconut consumption by TR occurred at *c.* 55 minutes in coconut clusters whereas an ecologically-relevant inflection point in coconut consumption based on time spent in coconut plantations was not achieved in BW despite a substantial sample size ($N_{BW} = 301$; Fig 7). In contrast, the number of unique individuals feeding on coconuts during a foray into a coconut plantation showed widely disparate association with number of coconuts consumed in the two groups, with TR exhibiting a slightly declining trend and BW showing a gradual incline (Adjusted $R^2_{TR} = 0.67$, $Sy_{XTR} = 1.08$; Adjusted $R^2_{BW} = 0.89$, $Sy_{XBW} = 0.29$; Fig. 7). The parameter estimates and associated goodness of fit measures for all the models are presented in Electronic Supplementary Material Table S3.

Discussion

The framework provided by the HIREC model (Sih *et al.* 2011) posits that species modify their behavior, or learn and undergo evolutionary adaptations to cope with changes in their ecology, explains our observations on the inclusion of coconut in the diet by the Nicobar long-tailed macaques. Although coconut was introduced to these islands two hundred years ago, there are still some macaque groups, which have had no exposure to coconut plantations, some groups have been recently exposed, and some have been living in and around coconut plantations

for a long time. These ecological conditions and the complexities and skills required for feeding on coconuts provided us an opportunity to understand foraging adaptations by the Nicobar long-tailed macaques. We found that the groups farther from coconut plantations are unfamiliar with coconuts and hence, do not feed on them. Groups in open vegetation closer to the coast with access to coconut plantations have a substantial dependence on coconuts, with the urban (coastal) group using coconuts less than the non-urban (coastal) group. Forest groups with very recent exposure to coconuts use them less. With a higher use of coconuts, coconut-dependent groups consistently select harder-to-process mature coconuts, whereas, due to lower use marginally coconut-dependent groups choose immature to very immature nuts. Coconut-dependent coastal groups show tight seasonality in coconut consumption with the wettest months recording higher consumption than the driest months. Coconut feeding occurs throughout the day during the wettest months and in the morning/evening during the driest months. Coconut consumption shows a quadratic relationship with number of feeding individuals and duration of time spent in palm plantations. Here, we discuss each of the main results in detail.

Coconut consumption by Temple Run, Baywatch and Forest Camp and their monthly trends

In agreement with our hypothesis, we found that groups in Category-1 have no familiarity with the coconut due to the absence of the palm in their rainforest habitat. The only response logged during the familiarity test was possibly from an adult or a sub-adult male, which had dispersed from a coconut-familiar group into a coconut-unfamiliar group. For groups that are exposed to coconuts only recently, such as the one in Category-3, *per capita* consumption of coconuts remained extremely low, and did not follow any consistent pattern, denoting virtually no dependence on the resource. As hypothesized, we found strong seasonality in coconut consumption by Category-2 and Category-4 despite the former being urban-dwelling and the latter being forest-dwelling and having access to alternative food resources. For the TR group, the alternate food resources included a wide variety of cultivars and/or synthetic food items and for BW, alternate food resources comprised several native varieties of fruits, flowers and shoots/leaves. The common feature between TR and BW that is possibly responsible for inducing a seasonal trend in coconut feeding is their coastal subsistence besides access to adequate coconuts. It is essential to note, however, that there was a phase shift in the annual cycle of coconut feeding between TR and BW by a month. Interestingly, the highest monthly consumption of coconuts by TR (i.e. September) during the two annual cycles coincided with the wettest month based on meteorological records during 2012–2018 of Campbell Bay, although August recorded the highest rainfall during the observation period. We did not find any such asynchrony between the driest month and month with the lowest coconut consumption in BW and thus, months with the highest and

the lowest coconut consumption coincided completely with the wettest and the driest months, respectively. Besides food-resource-based explanations, the most parsimonious explanation for enhanced coconut consumption during periods of relatively high rainfall are precipitation-mediated periodic dips in coastal temperature that facilitate foraging in open palm plantations by creating more favorable ambient temperatures. The results affirm local reports from plantation owners that coconut depredation by monkeys is disproportionately higher during periods of high rainfall.

Duration of time spent in coconut plantations by Temple Run and Baywatch

The higher use of coconut by BW relative to the rest of the groups was apparent in terms of the duration of time the group spent in coconut palm plantations. However, monthly patterns of foray duration did not coincide with the trend of coconut consumption in either group, leading to scenarios of low consumption despite extended forays and, conversely, instances of high consumption regardless of short forays. As a result, no seasonality was uncovered in the variable by the seasonality analyses. Apart from the contribution of alteration in the definition of entry/exit to coconut clusters in TR, disparities observed in the trend of the variable across both groups is a result of dependence of the group on services, such as refuge and food (in the form of insect pests and eggs of lizards or birds) provided by undefended portions of palm plantations. In abandoned or unmaintained parts of plantations, coconut palms occur with trees (such as *Pandanus odoratissimus* and *Terminalia catappa*) and herbs, offering additional food resources to the species leading to its regular use. The variable could nevertheless capture the difference in time spent in plantations by TR and BW, a proxy for time allocated to coconut foraging and hence, indirectly for coconut dependence. However, we still advocate exercising caution in use of the variable under violations discussed above (e.g., mixed cropping).

Phenophase of coconut consumed by Forest Camp and Baywatch

A disproportionately large number of immature coconuts of phenophase, P1 (75.4%) and P2 (16.6%) were consumed by FC group (which began coconut consumption approximately in the year 2014; more recently than BW) relative to BW group (P1 = 45.2%, P2 = 34.7%). The representation of the phenophase of coconuts on the consumption record of FC is reflective of the ease with which immature coconuts of very early stages can be dislodged and hence, was mastered in the available time period. The Zanzibar red colobus is also known to feed on immature coconuts (Siex and Struhsaker 1999), although the preference of resource parts (basal one-third portion of immature coconuts) is contrastingly different to the long-tailed macaque. Curiously, under an experimental setting, coconuts of higher phenophases (P3–P5) were

consumed exclusively by 1–2 adult males (of the 3–5 adult males) of the group raising the possibility that these individuals could have dispersed from coconut-dependent natal groups (Das *et al.*, in prep.). The meager number of coconuts of late phenophase recorded in FC might have emerged from these few males. In conclusion, the choice of phenophase is a veritable identifier of coconut dependence in a Nicobar long-tailed macaque group.

Dietary dependence of Temple Run on coconuts relative to other food resources

We analyzed the feeding ecology of the TR group since it was possible to observe foraging by this group throughout most of their range, which was not the case for the other groups. Inter-annual changes in the dietary contribution of principal resource items were marginal. The dietary contribution of coconut in TR declined by 7% in the second annual cycle but the proportion of plant-derived food items, including coconuts, remained almost constant at *c.* 0.67. The decline in coconut consumption is a result of a range-shift in response to territorial expansion by an adjacent group to areas with higher concentrations of managed green spaces such as gardens of residential quarters, offices and temples, as opposed to a matrix of forest, settlements and home gardens with the former having lower abundance of coconut palms than the latter. The remarkably high contribution of a single plant species (25–32%)—the coconut palm—in the diet of even an urban-ranging group is indicative of the importance of coconut to the species, or rather the group's dependence on the nut. The contribution of animal-derived food items marginally increased in the second annual cycle by 4%, whereas the contribution of synthetic items fell by 2% in the second annual cycle. The increment of animal-derived food items and the decrement of artificial food items could be the consequence of dietary compensation rather than a reflection of alteration in foraging habit and/or range shift. Although the limitations of our study did not allow us to compare proportionate consumption of coconuts across groups, Siex and Struhsaker (1999) found that red colobus monkeys consumed fewer coconuts in habitats where “higher densities and basal area of alternatives food sources” were available. Because TR has been part of behavioral research since 2013 (e.g., Velankar *et al.* 2016 and Pal *et al.* 2018), the chronological transformation of TR from a peri-urban group into an urban group as a result of competitive exclusion by a rival group was closely observed. As a result of this sustained displacement into an urban and/or altered landscape, the exotic component of TR's diet has surpassed the native component. Resource parts of common tropical plants found in the residential and the office gardens of Campbell Bay dominate the floral diet of the group similar to any generic group of urban nonhuman primate species (e.g., rhesus monkey and bonnet macaque), highlighting the widespread ecological homogenization of residential and urban spaces.

Hourly frequency of coconut foraging by Temple Run and Baywatch across the day

The temporal pattern of crop foraging by nonhuman primates is under-investigated in crop-related (nonhuman) primate-human “conflict” literature, perhaps because the nature and extent of crop depredation/damage is accorded higher priority from a management and mitigation perspective (e.g., McLennan 2008; Strum 2010; Wallace and Hill 2012). Moreover, a general opinion is often built about animal visits on the basis of statements made by farmers with limited emphasis on empirical validity (e.g., Saj *et al.* 2001). On averaging incidences of coconut foraging in a day across an annual cycle, both the focal groups showed no difference in coconut foraging across time slots except BW during the second annual cycle. The difference in temporal distribution of coconut foraging in BW is probably due to a deficit in data for a period of four months. The remarkable similarity in temporal uniformity between TR and BW despite their ecological differences could be a vital characteristic of coastal-living groups dependent on coconuts. Our results lend credence to why coconut horticulturists fail to identify specific time phases of coconut foraging by monkeys. However, consistent temporal segregation in coconut foraging (within a day) is observable if shorter time periods are considered, for example foraging occurred strictly either in the morning (05:00–10:00 h) and/or in the early evening (14:00–17:30 h) roughly during March to mid-June (dry months).

Based on our conjecture that the pattern of temporal foraging for coconuts would vary between the highest coconut-feeding months and the lowest coconut-feeding months as a result of accommodating large records of coconuts foraged/fed on, we pursued two independent lines of statistical reasoning. The first statistical testing ensuring paired comparison of time slots found difference between high feeding months and low feeding months in both groups, denoting similar responses in coconut-dependent groups. In the second statistical testing scenario using direct matched-pair test of time slots between the highest and the lowest feeding months, we found a stark difference as coconut foraging completely ceased between 11:01–15:30 h during the lowest feeding months whereas coconut consumption continued almost unabated through the day during the highest feeding months.

Pattern of relationship between time spent in coconut plantations and feeding individuals with coconut consumption in Temple Run and Baywatch groups

Expecting dissimilar quadratic relationships between coconut consumption and its determinants in the two groups, we analyzed them individually. Beginning with TR, we found a quadratic increase in coconut consumption with increase in time spent in palm clusters till approximately the first 20 minutes, followed by an inflection point after about an hour. It is evident, therefore, that in TR most coconut feeding is concentrated in the first 20 minutes of entry into a palm cluster. Likewise, an inflection point in coconut consumption is reached with eight foraging individuals with an effective group size of

just 12 individuals. A similar association is revealed between the duration of forays into palm plantations and coconut consumption in BW, with most coconuts fed on in approximately the first 125 minutes and the concavity of the curve achieved probably at about 12:08 h, both of which are substantially different from TR. Surprisingly, in negation of our hypothesis, the relationship between the strength of the feeding individuals and coconut consumption showed a quadratic incline as a result of sequential entry and feeding of coconuts instead of concurrent foraging. Serial foraging in palm plantations led to longer duration of visits and higher cumulative coconut consumption.

The scenario of foraging on a tough embedded fruit by Nicobar long-tailed macaques is particularly interesting in the context of dietary expansion since the species has no evolutionary history of feeding on any food item similar to the coconut. We conclude that a long and sustained exposure to a tough embedded food can stimulate a species with the aptitude for dietary and behavioral flexibility, manual dexterity, laterality and social learning to exploit the resource. The exploitation of embedded resources could occur as a result of “persistent and generative” object manipulation (Parker and Gibson 1977, 1979; Melin *et al.* 2014) under circumstances, such as the ones associated with insular subsistence (such as area of landmass, MacArthur and Wilson 1967; barrier to dispersal; spatiotemporal stochasticity of resources), habitat alterations, expansion of horticulture, anthropogenic changes and climate alterations (see Graham *et al.* 2017). Once motor sequences for processing the embedded resource emerge, transmit across conspecifics and become fixed, the species begins to gradually depend on the resource under favorable socioecological conditions. We presented data from groups across the gradient of dependence on coconuts; groups in Category-1 had no dependence on coconut as a result of absolute/partial unfamiliarity; the group in Category-3 had minimal dependence on coconut and consumed immature coconuts predominantly; groups of Category 2 and Category 3 had higher dependence on coconuts and BW did not alter coconut consumption on encountering resistance from humans, signifying either the high resource value of coconut or the degree of risk they are willing to endure (Hill 2017). Of particular concern, is the possibility of developing insensitivity and habituation towards crop-protection measures including adaptation to farmer behavior (as suggested by Wallace and Hill 2012) that can further escalate the situation and induce greater hostile/lethal interventions. Despite the distinct nature of their coastal habitats, TR and BW showed high dependence on coconuts, exhibited strict seasonality in consumption pattern and consistently chose mature coconuts regardless of their complexity and prolonged consumption time (>26 min at times), possibly due to a high energetic and nutritional return. Investigating probable cause(s) for the pattern of dependence on coconut and the associated functional value of the nut to the species as a source of nutrition and/or for thermoregulation would help formulate management strategies to reduce competition with humans.

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Supplementary Tables

Table S1. Summary and description of control and experimental phases of the coconut familiarity experiment conducted with three groups of macaques in Great Nicobar.

| Control Phase | | | | | | |
|--------------------|-------------|---------------------------|--------------------|--|-----------|------------|
| Group | Trial Index | Fruit species | Control Set-up | | Fed | |
| | | | # On path | # Off path | # On path | # Off path |
| Farthest | 1 | <i>Ficus auriculata</i> | 10 | 6 | 8 | 1 |
| | 2 | | 10 | 6 | 9 | 1 |
| Intermediate | 1 | <i>Spondias pinnata</i> | 9 | 5 | 9 | 0 |
| | 2 | | 9 | 5 | 8 | 0 |
| Closest | 1 | <i>Calamus dilarectus</i> | 10 | 6 | 7 | 2 |
| | 2 | | 10 | 6 | 6 | 1 |
| Experimental Phase | | | | | | |
| Group | Phenophase | Trial Index | # Coconuts on path | Fed/Displaced (Coconut 1-Coconut 2) (in m) | | |
| Farthest | P2 | P2-1 | 2 | -R* -R | | |
| | | P2-1' | 2 | 0/0-0 | | |
| | | P2-2 | 2 | 0/0-0 | | |
| | P6 | P6-1 | 2 | 0/0-0 | | |
| | | P6-2 | 2 | 0/0-0 | | |
| | | | | | | |
| Intermediate | P2 | P2-1 | 2 | 0/0-0 | | |
| | | P2-2 | 2 | 0/0-0 | | |
| | | | | | | |
| | P6 | P6-1 | 2 | 0/0-0 | | |
| | | P6-2 | 2 | 0/0-0 | | |
| | | | | | | |
| Closest | P2 | P2-1 | 1 | 0/0 | | |
| | | P2-2 | 1 | 0/0 | | |
| | P6 | P6-1 | 1 | 0/7 | | |
| | | P6-2 | 2 | 0/0-0 | | |

*Removed - Repeat trial

Table S2. Comparison of temporal distribution of foraging and feeding of coconuts through the day between the highest and the lowest coconut feeding months (FM), individually in Temple Run (TR) and Baywatch (BW) groups using generalized least square modeling fitted by using restricted maximum likelihood method (REML)

| Correlation structure/Troop | AIC | df | φ | Coefficients | Estimate | SE | t | p |
|---|--------|----|------|--------------|----------|-------|-------|---------|
| Model 1 Foraging and feeding of coconuts ~ FM + Time slot + FM*Time slot | | | | | | | | |
| None/TR | 198.54 | 52 | NA | Intercept | 4.81 | 1.08 | 4.43 | <0.0001 |
| | | | | FM | -1.27 | 0.69 | -1.85 | 0.07 |
| | | | | Time slot | -0.004 | 0.002 | -1.75 | 0.09 |
| | | | | FM*Time slot | 0.002 | 0.001 | 1.51 | 0.14 |
| AR(1)/TR | 196.15 | 52 | 0.33 | Intercept | 4.75 | 1.54 | 3.09 | 0.003 |
| | | | | FM | -1.20 | 0.97 | -1.24 | 0.22 |
| | | | | Time slot | -0.004 | 0.003 | -1.15 | 0.26 |
| | | | | FM*Time slot | 0.002 | 0.002 | 0.92 | 0.36 |
| AR(1 Time)/TR | 198.77 | 52 | 0.27 | Intercept | 4.81 | 0.96 | 4.99 | <0.0001 |
| | | | | FM | -1.27 | 0.59 | -2.16 | 0.04 |
| | | | | Time slot | -0.004 | 0.002 | -1.97 | 0.05 |
| | | | | FM*Time slot | 0.002 | 0.001 | 1.77 | 0.08 |
| None/BW | 336.88 | 52 | NA | Intercept | 13.27 | 4.58 | 2.89 | 0.006 |
| | | | | FM | -6.21 | 2.90 | -2.14 | 0.04 |
| | | | | Time slot | -0.01 | 0.01 | -1.38 | 0.17 |
| | | | | FM*Time slot | 0.01 | 0.006 | 1.72 | 0.09 |
| AR(1)/BW | 334.27 | 52 | 0.33 | Intercept | 13.05 | 6.44 | 2.03 | 0.05 |
| | | | | FM | -5.89 | 4.08 | -1.44 | 0.16 |
| | | | | Time slot | -0.01 | 0.01 | -0.95 | 0.35 |
| | | | | FM*Time slot | 0.01 | 0.01 | 1.12 | 0.27 |
| AR(1 Time)/BW | 338.88 | 52 | 0.01 | Intercept | 13.27 | 4.56 | 2.91 | 0.001 |
| | | | | FM | -6.21 | 2.88 | -2.16 | 0.04 |
| | | | | Time slot | -0.01 | 0.009 | -1.39 | 0.17 |
| | | | | FM*Time slot | 0.01 | 0.006 | 1.73 | 0.09 |

Table S3. Summary of quadratic regression models with ‘coconut consumed’ per foray into coconut cluster/plantation as the dependent variable and either, duration of ‘time spent in plantation/cluster’ per visit (Dur) and number of ‘unique individuals feeding coconuts’ (Ind) as the independent variable, each for TR and for BW. General expression of quadratic function: $y = B_0 + B_1x + B_2x^2$

| Variable | Troop | df | N | SS | RMSE | Outlier | Coeff | Estimate | 95% CI |
|------------------------|-------|-----|-----|-------|-------|----------|----------------|-----------|-----------------|
| Dur | TR | 242 | 245 | 550.3 | 1.50 | 0 (*Q=1) | B ₀ | 2.673 | 2.465-2.882 |
| | | | | | | | B ₁ | 0.142 | 0.117-0.167 |
| | | | | | | | B ₂ | -0.001 | -0.002--0.001 |
| Ind (#X ²) | TR | 185 | 188 | 215.4 | 1.07 | 0 (Q=1) | B ₀ | 2.140 | 1.975-2.305 |
| | | | | | | | B ₁ | 0.269 | 0.226-0.311 |
| | | | | | | | B ₂ | -0.002 | -0.003--0.001 |
| Dur (Y ⁻¹) | BW | 294 | 297 | 1484 | 11.59 | 22 (Q=2) | B ₀ | 25.450 | 23.010-25.960 |
| | | | | | | | B ₁ | 0.193 | 0.151-0.188 |
| | | | | | | | B ₂ | -1.159e-4 | -2.2e-4--6.4e-5 |
| Ind (Y ⁻²) | BW | 153 | 156 | 13.13 | 0.29 | 0 (Q=1) | B ₀ | 20.150 | 19.860-24.110 |
| | | | | | | | B ₁ | 2.260 | 2.174-2.672 |
| | | | | | | | B ₂ | 0.047 | 0.033-0.063 |

*ROUT coefficient #Mathematical transformation