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Use of an embedded fruit by Nicobar Long-tailed Macaque *Macaca fascicularis umbrosus*: II. Demographic influences on choices of coconuts *Cocos nucifera* and pattern of forays to palm plantations

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Abstract: Adaptive pressures of human-induced rapid environmental changes and insular ecological conditions have led to behavioral innovations among behaviorally flexible nonhuman primates. Documenting long-term responses of threatened populations is vital for our understanding of species and location-specific adaptive capacities under fluctuating equilibrium. The Nicobar Long-tailed Macaque *Macaca fascicularis umbrosus*, an insular sub-species uses coconuts *Cocos nucifera*, an embedded cultivar as a food resource and is speculated to have enhanced its dependence as a result of anthropogenic and environmental alterations. We explored demographic patterns of use and abandonment of different phenophases of fresh coconuts. To study crop foraging strategies, we recorded daily entry and duration of forays into coconut plantations. We divided age-classes into early juvenile (13–36 months), late juvenile (37–72 months), and adults (>72 months) and classified phenophase of coconuts into six types. Consistent with the theory of life history strategies, late juveniles were found to use a greater number of coconuts, which was considerably higher in an urban troop but marginally higher in a forest-plantation dwelling group. Except in late juveniles, males consumed a higher number of coconuts than females in the remaining age-classes. Owing to developmental constraints, juveniles of both types used higher proportion of immature coconuts though adults showed equitable distribution across phenophases. Pattern of entries to plantations and duration of forays were uniform through the day in the urban troop but modulatory in the forest-plantation group, perhaps due to frequent and hostile human interferences. Observations corroborating adaptations to anthropogenic disturbances are described.

Keywords: Coconut phenophases, hard to process food, human-induced rapid environmental change, human-macaque competition, dependence on coconut, coconut-based resource competition, coconut consumption, Nicobar archipelago

INTRODUCTION

Among the many challenges that primates and their habitats face globally, rapid and escalating anthropogenic changes in the age of the Anthropocene are having an irreversible effect on primate populations leading to exclusion, extinction (~60% of primate species, Estrada et al. 2017) and severe constriction of ranges in most primate species (~75% of primate species), (Estrada et al. 2017; Erinjery et al. 2017; Kalbitzer & Chapman 2018). Although a few dietary and habitat generalist primate species are beginning to show indication of behavioural adaptation to anthropogenic habitats (McLennan et al. 2017; Santini et al. 2019), many specialist primate species are trapped in their ecological niches constrained by their phylogeny, life-history, physiology and/or limited phenotypic plasticity (Vázquez & Simberloff 2002; Fisher & Owens 2004; Kalbitzer & Chapman 2018). Even among populations that are synanthropic/commensal to humans, many studies have enunciated the impact of habitat modification on a variety of socioecological (Back et al. 2019), parasitological (Kouassi et al. 2015; Zanzani et al. 2016; Kumar et al. 2018;) and health variables (Kaur et al. 2008; Muehlenbein et al. 2010). Many flexible populations of Apes, Old and New world primate populations subsisting in anthropogenic habitats especially of the genus, *Pan*, *Macaca*, *Papio*, *Cebus*, *Cholorcebus*, and *Saimiri* exhibit evidences of compensating for dietary stress with expansion of dietary resources (like crops and synthetic foods) and associated supplemental foraging strategies (*Pan*, Hockings et al. 2015; *Macaca*, Ilham et al. 2017; Brotcorne et al. 2017; *Papio*, Fehlmann et al. 2017; *Cebus*, Back et al. 2019; *Cholorcebus*, Thatcher et al. 2020; *Samiri*, Campêlo et al. 2019). Many of such food-enhanced populations show complex sensorimotor intelligence associated with extraction of embedded food resources and feed on food items novel to their ancestral diet (e.g., oil-palm nut processing by Burmese Long-tailed Macaque, Luncz et al. 2017).

Alongside many novel frugivore-fruit relationships, the relationship between the Nicobar Long-tailed Macaque *Macaca fascicularis umbrosus* (Images 1,2) and the coconut *Cocos nucifera L.*, a perennial cash crop is particularly intriguing since both the species have colonised the Nicobar archipelago of the Andaman & Nicobar Islands. Although the nature of dependence of the macaque species on wild varieties of coconuts occurring in the islands is unknown, domesticated land races of coconuts have arrived on the island ~2,250 years ago (see Gunn et al. 2011; Niral & Jerard

2018). Groups of macaques closest to coconut palm plantations are exposed to the drupe and thus, familiar to 'domesticated' coconuts and coastal groups that have had prolonged exposure to coconut palms have a much higher dependence than recently exposed inland groups (Das et al. 2020). Systematic destruction of habitats for expansion of coconut horticulture and agriculture (Arora 2018), human habitations and defence establishments along with environmental changes/catastrophes (aridity/Indian ocean tsunami) have disproportionately affected groups on the edge of their habitats (Karnauskas et al. 2016; Reddy 2018), constituted largely by coastal populations of long-tailed macaques (Umapathy et al. 2003; Velankar et al. 2016). Under such circumstances, it becomes essential to study the adaptive pressures of both, gradual and extreme habitat alterations on coastal populations and the resultant behavioural responses, especially in context of dietary expansion and foraging innovations. Since, many such dietary adaptations can have adverse effects on survival and/or persistence of a species in an agriculture ecotone especially, if these resources are shared or cultivated by humans (Hockings et al. 2015; Hill 2017; Kalbitzer & Chapman 2018), it becomes vital to study behavioural flexibilities to explicate adaptive capacities of species and/or population(s) experiencing anthropogenic pressures. Behavioural flexibilities within a group, however, are not expressed identically across demographic classes and age-sex class-specific strategies prevail as a result of distinct life histories (Stamps & Krishnan 2017). For instance, studying the dynamics of group fission in Sumatran Long-tailed Monkey, van Schaik & Noordwijk (1985) described age and social affiliation-specific disintegration of foraging parties with large-bodied sub-adults foraging solitarily during fruiting seasons. Even size and hardness of fruits fed varied along the age-sex axes (van Schaik & Noordwijk 1985). Although many sub-species of long-tailed macaques have been documented to feed on complex embedded resources (like *Opuntia* spp., Tan et al. 2016; *Terminalia catappa*, Falótico et al. 2017; *Elaeis guineensis*, Proffitt et al. 2018) including usage of stone tools to access few of them, variation in the use of these resource items along demographic axes has been seldom investigated (c.f. intertidal shellfishes, Gumert et al. 2011). We adopted the HIREC framework (human-induced rapid environmental change) expounded by Sih et al. (2016) to understand adaptive pressures specific to individual species along with commensurate dietary flexibilities, adaptive potential, and overall phenotypic flexibility in response to extreme anthropogenic

Image 1. Adult females of Nicobar Long-tailed Macaque *Macaca fascicularis umbrosus* (Temple Run group) seated on the wall of a temple complex enclosing a small cluster of coconut palms. © Reshma, P.B., Research Asssitant, Nicobar Project.

Image 2. A juvenile female of Nicobar Long-tailed Macaque Macaca fascicularis umbrosus (Baywatch group) feeding on coconut kernel. © Sayantan Das.

changes to ecosystems. We estimated that the severity of HIREC would be compounded in an insular condition due to the ecological fragility of island ecosystems leading to the exertion of stronger adaptive pressures on coastal groups of long-tailed macaques than on inland/mainland groups (e.g., many island populations of long-tailed macaques (e.g., Malaivijitnond et al. 2007; Luncz et al. 2017) and capuchin monkeys show tool-use behavior (e.g., Barrett et al. 2018)). Despite phylogenetic constraints on expression of behavior, we expected insular populations of long-tailed macaques to express greater behavioral flexibility, quicker learning, proficient extractive foraging and greater tendency of dietary expansion (e.g., Malaivijitnond et al. 2007; Tan et al. 2015, 2016). Thus, the human-macaque interface in the heterogeneous habitat of Nicobar Islands creates a virtual experimental condition for studying emergence of foraging and other dietary adaptations and/or innovations under conditions of HIREC.

In the current study, we focused on how demographic categories, i.e., age and sex compared to each other and to other similar groups in their use of phenophase of coconuts. We also aimed to study contingent acquisition and abandonment of coconuts by age-classes and describe their probable causes. Based on the theory of life-history strategies in macaques, we hypothesized that older juveniles (3–6 yrs) would feed on the highest number of coconuts followed by adults (>6yrs) and younger juveniles (1–3 yrs) due to the largest energy requirement of older juveniles among all age-classes. Comparison of the two sexes though is less straightforward since both, reproductive females and adult males have high energetic requirements for

procreation and for maintenance of larger body size, respectively (e.g., Collins 1984; van Schaik & Noordwijk 1985). Since procreation lasts for a shorter time scale than body maintenance, we expected adult males to feed on a higher number of coconuts than adult males. For the remaining age classes, we expected no difference between the two sexes. Because the husk and the shell of the coconut gets progressively tougher and harder with development, we expected adults to process higher number of mature coconuts than by juveniles though tender coconuts will continue to be preferred choices by all age-classes due to the ease of extractive processing.

The marginal value theorem (MVT) within optimal foraging theory postulates that the time spent in resource patches by individuals/groups follows maximization of net energy, i.e., the difference in energy invested in foraging and the energy gained by ingestion (Pyke et al. 1977; Charnov & Orians 2006). Group-level patterns of decisions pertaining cultivar use and plantation visitation is comprehensively specified by MVT, which assumes a greater prominence when conjoined to the HIREC framework since cultivar (resource) attractiveness, cultivar (resource) value and risks from human and non-human crop defenders are introduced as additional factors. In this study, we were interested in expounding and contrasting patch entry and patch use by two groups with different degrees of coconut-dependence, different experiences of human hostilities and different distribution of coconuts, throughout the day. A secondary intent was to generate data that would serve as a baseline for more detailed studies on movement and foraging decisions in contested landscapes. Further, we used the MVT framework within HIREC to obtain insights into the processes governing entry/exit and patch usage dynamics of the focal groups.

METHODS

Study site

We undertook the study at Great Nicobar and Katchal in the Nicobar archipelago of Andaman & Nicobar Islands lying between 93.634–93.953E & 6.735–7.229N, and 93.301–93.475E & 7.873–8.026N, respectively (Figure 1). The major forest types in these islands are the Andaman tropical evergreen forest and the Andaman semi-evergreen forest (India State of Forest Report 2019). Due to their isolation from continental mainland, the islands have high degree of endemism with an extremely poor mammalian diversity (Nayar & Shastry 1987; Balakrishnan 1989; Rao 1989). The Nicobar Long-tailed Macaque is found across all vegetation types in the archipelago including littoral beach formations, mangrove vegetations on coastal regions, low land swamps and inland wet evergreen vegetations (Hajra et al. 1999; Arora 2018). Over the past century, unregulated phases of human migrations and unsustainable developmental initiatives have led to large-scale deforestation on the eastern coast of the islands altering local climatic conditions and threatening biodiversity. Human settlements, agricultural/production landscapes and other human-dominated spaces on the eastern coast are the primary centers of human-macaque hostilities (Rajeshkumar 2017). We chose to study coastal groups of Nicobar Long-tailed Macaque in the two islands that ranged within human-dominated spaces and showed considerable dependence on anthropogenic food resources.

Study groups

We studied two groups of long-tailed macaques, one in each island. The study groups ranged in coastal areas of the two islands. The first group, Temple Run (TR) subsisted within a matrix of semi-urban area, patchily-distributed native vegetation, advanced secondary forest and home garden/plantation of Campbell Bay town in Great Nicobar. Coconut palms occurred in sparse numbers within small (0.04ha) to moderate-sized gardens (0.5ha) maintained at government offices,
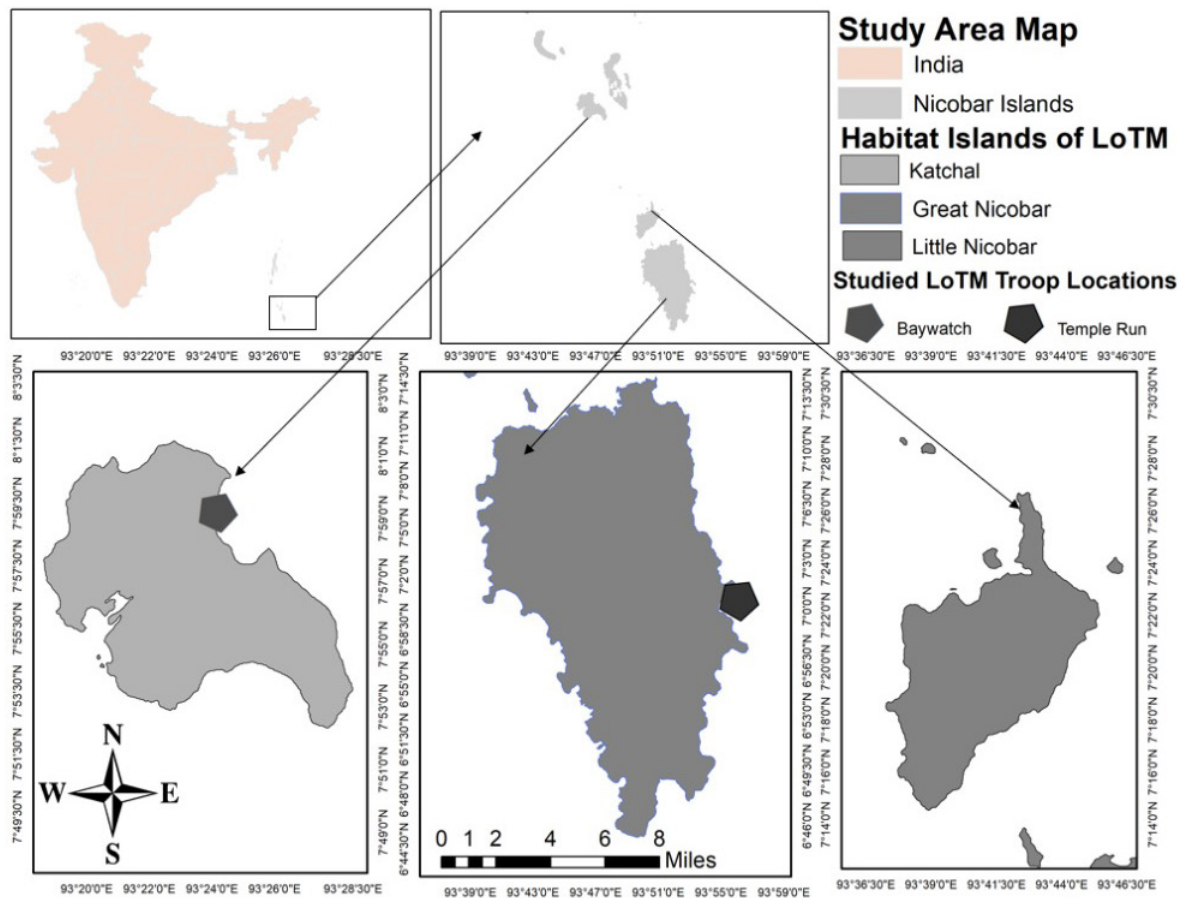

Figure 1. Depiction of the study area showing the distribution of Nicobar long-tailed macaque in the Nicobar islands of India alongside location of the two study groups.

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residential areas, temples and other public spaces. Therefore, TR had access to coconuts almost throughout the day (see Das et al. 2020). The second group, Baywatch (BW) used a cumulative coconut plantation area of 5.75ha spread across three patches that ran along the northeastern coast of Katchal. Alongside, the group also accessed semi-altered mixed evergreen forest and other coastal native vegetations. The group had six of (probably) seven–eight sleeping sites adjacent to palm plantations and largely consumed coconut at dawn and dusk. For information on the demographic structure of the two groups, see Das et al. (2020). The troops used coconuts considerably in general and used tougher and mature coconuts consistently, in specific. Conclusively, the troops displayed remarkable proficiencies in extractive foraging of coconuts signifying a long and an involved relationship with the nut, however, both the troops faced immense hostility from humans/dogs within agricultural and other anthropogenic landscapes as a result of crop depredation. Even so, active dispelling of macaques of both troops neither had an effect on their daily allocation of time spent in coconut plantation nor on daily coconut consumption (Das et al. 2020).

Field methods

Post habituation of the two groups, we began data collection from March 2018 for a period of 24 months and 20 months for TR and for BW, respectively. We followed TR from March 2018 to February 2020 and BW from March 2018 to October 2019. We divided the observation period into two annual cycles which began in March and ended in February as a result of the annual periodicity in coconut consumption (see Das et al. 2020). Due to our failure to identify immature individuals of TR group in the first annual cycle of the study, we report the results from the second annual cycle alone. Groups were followed from dawn to dusk at least once a week and for a minimum of five days in a month with sampling day considered as successful only if all coconuts acquired by a troop were accounted for. We noted coconut acquisition by the groups within an *all occurrence* behavioral sampling framework with each session continuing for 10 minutes. We recorded entry and exit schedules into coconut palm plantations of the troops, acquisitions of fresh coconuts from direct (from palm) and indirect (from other individuals and from ground) sources followed by their respective fates, i.e., either processed (if liquid endosperm is accessed) or unprocessed (if liquid endosperm is not accessed) and finally, age and sex classes of individuals (wherever possible) acquiring them. The sampling challenges

presented by the two troops as a result of the habitats they occupied led to minor difference in the field protocol followed. This included an inability to record phenophases of coconuts acquired by TR group as a result of inaccessibility to coconut palms. For description of the six phenophases of coconut and their identifying features, see Das et al. (2020). We combined the third and the fourth phenophases due to similarities in their developmental characteristics and for the purpose of easier representation. Demography of the two groups was assessed on a monthly basis.

Data analysis

We classified the life span of Nicobar Long-tailed Macaques into three classes, 13–36 months (early juveniles, EJ), 37–72 months (late juveniles, LJ) and >72 months (Adult, AD) based approximately on (1) coconut handling/processing proficiency and on (2) conventional age classifications for Macaques. We assessed the age-classes of individuals on a monthly basis. For the purpose of testing inter-annual consistencies, we partitioned the dataset of BW into the two annual cycles described previously and presented data of TR over a single annual period only. Whereas, to contrast temporal visit patterns to palm plantations (within a day) by TR with BW, we averaged data across the two annual cycles and represented them as 'frequency of entry' during 10 minutes slots along with corresponding time spent in plantations.

Unprocessed coconuts emerge when macaques acquire coconuts directly (from palm or ground) or indirectly (snatch from a conspecific) but leave them unfed as a result of unsuitability of coconut (i.e., coconut is diseased/disfigured/barren), incapability to process, mishandling (slippage while on the palm), imminent threat (sudden appearance of human/dog), probable satiation or other indecipherable reasons (for e.g., young juveniles can indiscriminately pluck coconuts when learning the technique of 'plucking and dislodging coconuts'). We expressed consumption and abandonment of coconuts in two different units across three temporal scales, 1) as proportion in an annual coconut consumption cycle, 2) as *per capita* mean in a month, and 3) as *per capita* mean throughout the study. Similarly, coconuts used by BW was expressed in two ways to reflect 1) overall share of different phenophases of coconuts and 2) proportionate share of different phenophases of coconuts within demographic classes. We compared (1) proportion data using Chi-squared test of multiple proportion and (2) *per capita* figures across demographic classes, months, annual feeding cycles and

groups using parametric/non-parametric comparison of means/ranks between two (e.g., t-test, Mann-Whitney U test) or more groups (e.g., ANOVA, Kruskal-Wallis test). All statistical analyses in this section were carried out using GraphPad Prism v.8.3.1 (GraphPad Software 2020).

To test seasonality of coconut use by the demographic classes, we fitted monthly *per capita* figures with the standard equation for seasonality $y = \alpha + \beta\sin(2\pi t) + \gamma\cos(2\pi t) + \varepsilon$. In order to test the hypothesis that (1) males have an overall greater consumption of processed coconuts than females and (2) that late juveniles disproportionately determined use of processed coconuts, we used a mixed effects modeling approach using maximum likelihood estimation with Laplace approximation. We used coconuts consumed by a demographic class (during a sampling day) as the dependent variable, month of sampling as the random factor and group identity, age-class (computed monthly) and sex as the fixed factors. To control for number of individuals in a given demographic class, we used an offset term, log (#of individuals). As a result of the versatile computing ability of the R Statistical Programming Language, we used RStudio v.1.3 (RStudio Team 2020) for all statistical analyses discussed in this section.

Finally, we illustrated frequency of entry to coconut plantation across the day and represented duration of time spent by a group on entry at a given time slot as mean ±SD. To depict trends, we used a fifth order polynomial equation. We plotted frequency of entry to coconut palm plantation alongside corresponding duration of time spent in the plantation by collating data from across all sampling days. All graphical illustrations were carried out in GraphPad Prism v.8.3.1 (GraphPad Software 2020).

Ethical note

The present study was exclusively observational and did not involve any invasive or controlled experimentation. Clearance for the observational protocol was received from the Institutional Animal Ethics Committee of the University of Mysore and complied with the Code of Best Practices for Field Primatology.

RESULTS

We undertook a total of 75 and 134 successful field samplings during a period of 12 and 20 months during which we recorded a cumulative of 746 and 7,382 processed coconuts, and 243 and 566 unprocessed
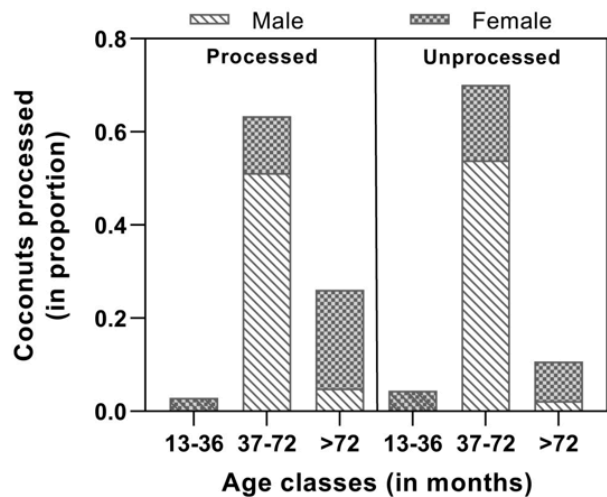

Figure 2. Representation of demographic classes in the sample of processed and unprocessed coconuts recorded in the Temple Run group during March 2019–February 2020. The sex classes within each age-class are demarcated.

coconuts in TR and in BW, respectively. Since a considerable proportion of data emerged from scanning as opposed to direct observations, information on demographic identity of the processing individual could not be established. Hence, the dataset used for demographic comparisons comprised a slightly smaller subset. We found evidences for variation in the use of coconuts across the gradients of age, sex, group, and month (see Das et al. 2020). We describe the results of this study below.

Age-specific acquisition of processed and unprocessed coconuts by Temple Run group in a single annual cycle and by Baywatch group in two consecutive annual cycles

We found contrasting results in the demographic shares of processed coconuts between TR and BW groups though coconuts left unprocessed by the two groups showed similar trends. With an aggregate EJ:LJ:AD ratio of 4:5.8:5.5 TR showed the following crude order of coconuts processed, LJ>AD>EJ ($\chi^{2,TR}_{LJ>AD}$=267.17, df=1, p<0.0001; $\chi^{2,TR}_{EJ<AD}$=119.03, df=1, p<0.0001; $\chi^{2}_{EJ<LJ}$=1148.16, df=1, p<0.0001; Figure 2). On the contrary, with an aggregate EJ:LJ:AD ratio of 8:6.6:14 and 11.3:10.2:14 during the first (AC-1) and the second annual cycles (AC-2), respectively, BW exhibited the following order of demographic classes in the number of coconuts processed, AD>LJ>EJ ($\chi^{2,AC-1}_{AD>LJ}$=408.73, df=1, p<0.0001; $\chi^{2,AC-1}_{LJ>EJ}$=287.28, df=1, p<0.0001; $\chi^{2,AC-1}_{AD>EJ}$=1532.14, df=1, p<0.0001: $\chi^{2,AC-2}_{AD>LJ}$=84.67, df=1, p<0.0001; $\chi^{2,AC-2}_{LJ>EJ}$=1128.32, df=1, p<0.0001; $\chi^{2,AC-2}_{AD>EJ}$=2027.09, df=1, p<0.0001; see Figure 3). An indicator of resources un-utilized and perceived crop depredation
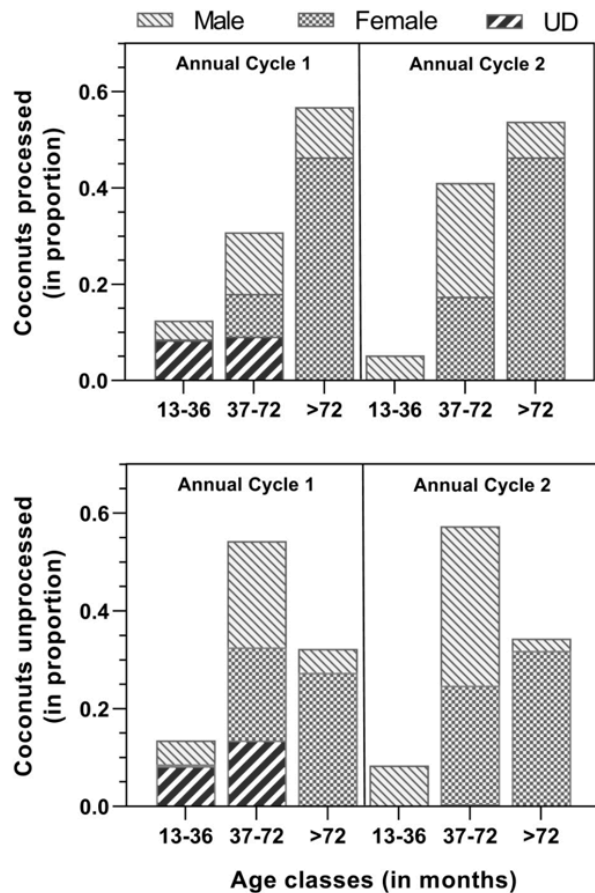
Figure 3. Representation of demographic classes in the sample of processed (top) and unprocessed coconuts (bottom) recorded in the Temple Run group during March 2018–October 2019. The sex classes within each age-class are demarcated.
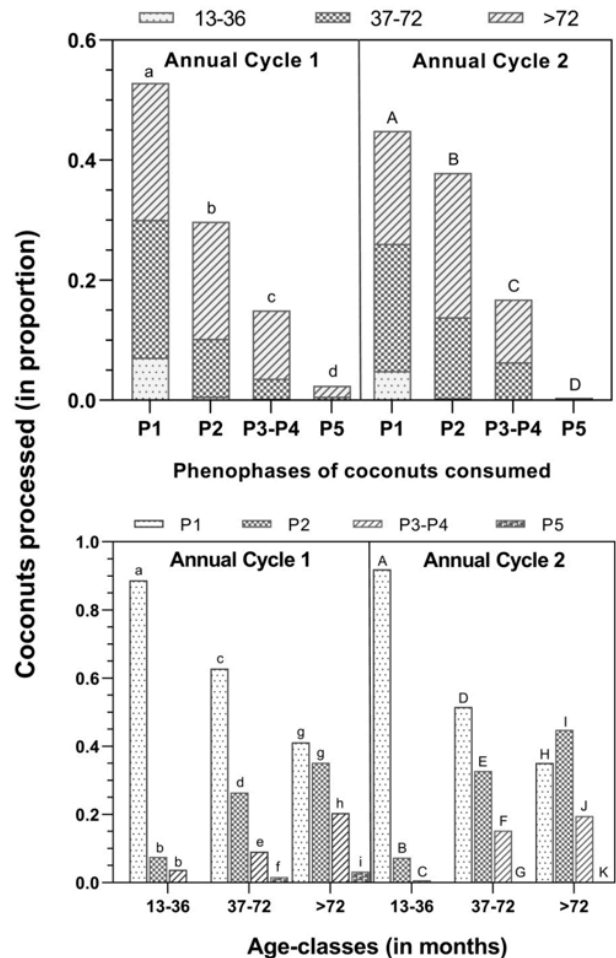

Figure 4. Relative use of processed coconuts by Baywatch group expressed as overall proportions of phenophases with demarcations of age-classes (top) and age class-specific proportions of phenophases (bottom). Note that the y-axes of the two graphs is identical but the x-axes are different.

by coconut horticulturists, the number of coconuts left unprocessed were also assessed in a similar manner. We found late juveniles to be the highest contributors to unprocessed coconuts across both troops and across both annual cycles (in BW) coherently followed by adults and early juveniles ($\chi^{2,TR}_{LJ>AD}$=313.49, df=1, p<0.0001; $\chi^{2,TR}_{EJ<AD}$=7.73, df=1, p=0.02; $\chi^{2}_{EJ<LJ}$=464.18, df=1, p<0.0001: $\chi^{2,AC-1}_{LJ>AD}$=34.09, df=1, p<0.0001; $\chi^{2,AC-1}_{EJ<LJ}$=148.70, df=1, p<0.0001; $\chi^{2,AC-1}_{EJ<AD}$=34.06, df=1, p<0.0001: $\chi^{2,AC-2}_{LJ>AD}$=26.92, df=1, p<0.0001; $\chi^{2,AC-2}_{EJ<LJ}$=178.25, df=1, p<0.0001; $\chi^{2,AC-2}_{EJ<AD}$=53.25, df=1, p<0.0001). In absolute terms, late juveniles in TR abandoned coconuts 5.6 times more than adults and 17.5 times more than early juveniles. Late juveniles in BW discarded coconuts 1.69 times and 1.67 times more than adults in the first and the second annual cycles, respectively, and 4 times and 6.8 times more than early juveniles in the first and the second annual cycles, respectively. Sex-specific shares of coconut consumption across each demographic class are also presented in Figure 2 and in Figure 3.

Use of different phenophases of processed coconuts by Baywatch group expressed as overall proportions and as demographic class-specific proportions across two annual cycles

A stable pattern was revealed in phenophases of coconuts used across both annual cycles. The order of phenophases use emerged to be the following P1>P2>P3/P4>P5 ($\chi^{2,AC-1}_{Overall}$=497.92, df=3, p<0.0001; $\chi^{2,AC-2}_{Overall}$=1684.94, df=3, p<0.0001) (Figure 4). Comparison of absolute figures of phenophases consumed in the first annual cycle revealed P1 to be consumed more than P2 by a factor of 1.8, more than P3 by a factor of 3.5 and finally, more than P5 by a factor of 21.8 times. Similar figures in the second annual cycle differed by a small margin with P1 consumed 1.2 times more than P2, 2.67 times more than P3/P4 and finally, 104.6 times more than P5. Depiction of stacked columns of coconuts

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processed by the demographic-classes in the first graph of Figure 4 is for visual illustration alone.

To determine choice of phenophase of processed coconuts used by a demographic class, we plotted the second graph of Figure 4. Note that the proportions within each age-class add to unity. Individuals in the age-class of 13–36 months, i.e., early juveniles fed a disproportionately low number of P2 (7.5%) and P3 coconuts (3.8%) relative to P1 (88.7%) coconuts with no representation of P5 coconuts. Early juveniles showed the following order of preference based on the number of coconuts processed, P1>P2=P3/P4 ($\chi^{2,AC-1}_{Overall,EI}$=153.63, df=3, $p<0.0001$) and P1>P2>P3/P4 ($\chi^{2,AC-2}_{Overall,EJ}$=435.37, df=3, $p<0.0001$) during the first and the second annual cycles, respectively. Late juveniles of the next age category fed on all classes of phenophase and had the following sequence of preference, P1>P2>P3/P4>P5($\chi^{2,AC-1}_{Overall,LJ}$=287.80, df=3, $p<0.0001$; $\chi^{2,AC-2}_{Overall,LJ}$=823.60, df=3, $p<0.0001$) across both annual cycles. Proportion of P1 and P5 coconuts processed by late juveniles decreased from 62.8% to 51.6% and from 1.7% to 0.4%, respectively whereas proportion of P2 and P3/P4 processed coconuts increased from 26.4% to 32.8% and from 9.1% to 15.3%, respectively. Finally, adults exhibited slight variability in their choice of coconuts across the two annual cycles displaying the following order of preference, P1=P2>P3/P4>P5 ($\chi^{2,AC-1}_{Overall,AD}$=167.68, df=3, $p<0.0001$) in the first feeding cycle and the order, P2<P1>P3/P4>P5 ($\chi^{2,AC-2}_{Overall,AD}$=824.94, df=3, $p<0.0001$) in the second feeding cycle (Figure 4). Corresponding alterations in the proportionate consumption of different phenophases of coconuts between the two annual cycles also became apparent, for example increase in use of P1, P3/P4 and P5 coconuts from 35.1% to 41.1%, from 19.5% to 20.4% and from 0.5% to 3.3%, respectively and decline in the use of P2 coconuts from 44.9% in the first annual cycle to 35.1% in the second annual cycle.

Abandonment of different phenophases of coconuts (unprocessed) by Baywatch group expressed as overall proportions and as demographic class-specific proportions

We found all phenophases of coconuts represented in the unprocessed category of coconuts. We found that the phenophase(s) that is/are processed the most is/are also the one(s) that is/are left unprocessed the most; we found P1(50%) to be the highest unprocessed coconut in the first annual cycle ($\chi^{2,AC-1}_{Overall,P1}$=36.86, df=3, $p<0.0001$) whereas both, P1(42.4%) and P2(30.9%) emerged as the phenophases with the highest unprocessed coconut in the second annual cycle ($\chi^{2,AC-2}_{Overall}$=95.59, df=3, $p<0.0001$; $\chi^{2,AC-2}_{P1=P2}$=6.75, df=1, $p=0.08$). The order of the remaining
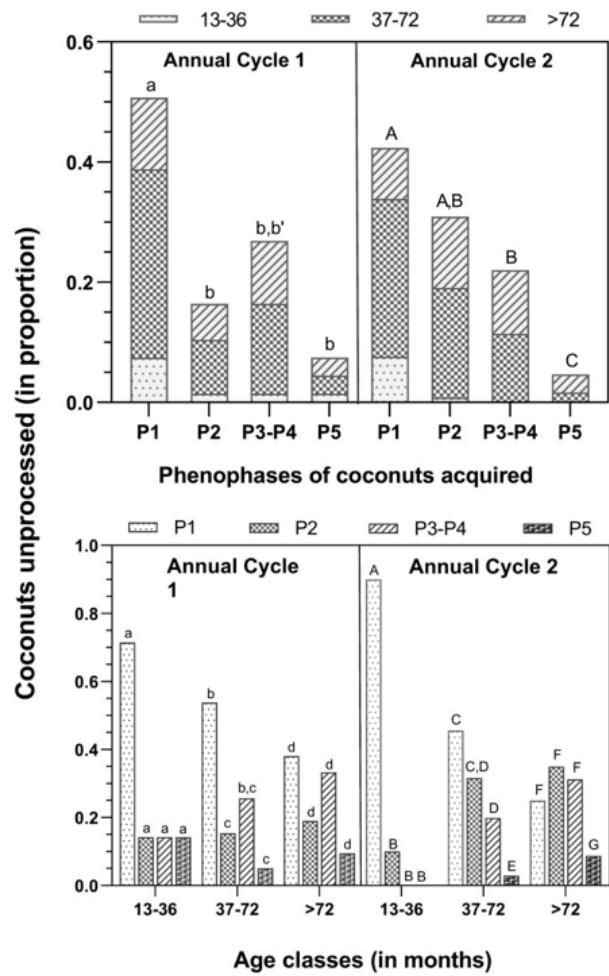

Figure 5. Relative abandonment of unprocessed coconuts by Baywatch group expressed as overall proportions of phenophases with demarcations of age-classes (top) and age class-specific proportions of phenophases (bottom). Note that the y-axes of the 2 graphs is identical but the x-axes are different.

phenophases did not show any consistent pattern across the annual cycles. In the first annual cycle, the proportion of P3/P4(26.5%) coconuts left unprocessed was higher than P5 (7.4%) ($\chi^{2,AC-1}_{P3-P4>P5}$=9.46, df=1, $p<0.0001$) but equivalent to P2(16.2%) ($\chi^{2,AC-1}_{P3-P4=P2}$=2.18, df=1, $p=0.54$) whereas the proportion of P2 coconuts left unprocessed was comparable to P5 ($\chi^{2,AC-1}_{P2=P5}$=2.60, df=1, $p=0.46$). In the next annual cycle, we obtained the following order of phenophases, P3/P4(22.03%) > P5(4.66%) coconuts ($\chi^{2,AC-2}_{P3-P4>P5}$=32.94, df=1, $p<0.0001$) (Figure 5).

As opposed to processed coconuts, all the phenophases were represented in unprocessed coconuts across all the demographic classes. On analyzing the proportion of phenophases of coconuts left unprocessed by individual demographic classes across the annual cycles, we found that the highest processed phenophase emerged as the highest unprocessed coconut in the
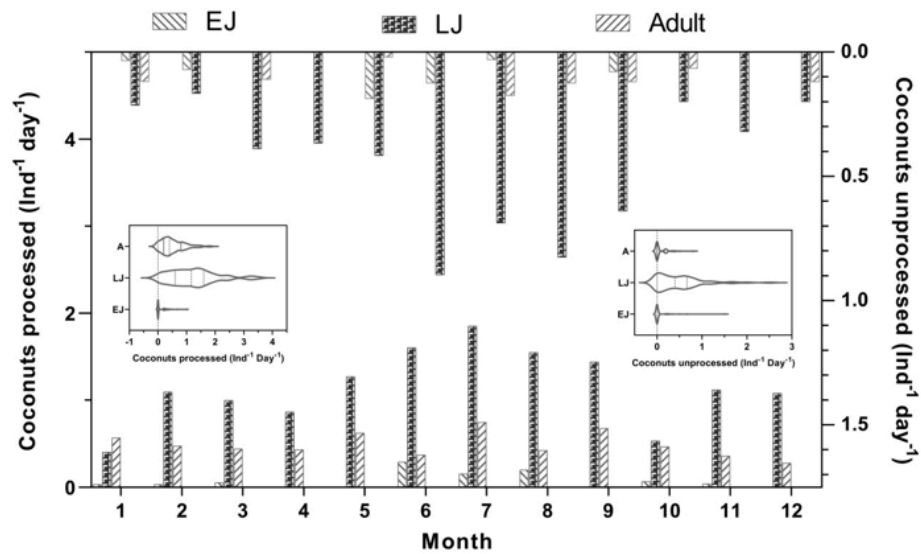
JOTT

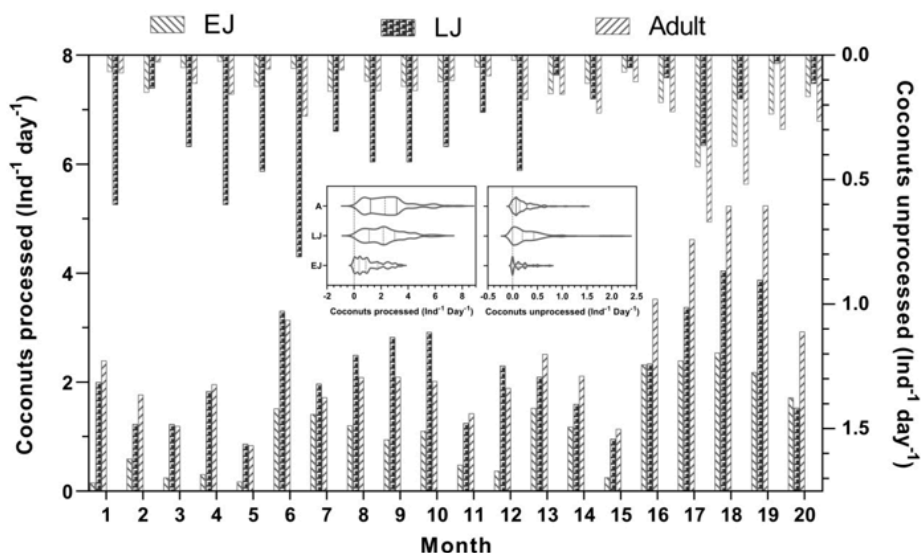Use of an embedded fruit by Nicobar Long-tailed Macaque   Das et al.

Figure 6. Monthly *per capita* use of processed coconuts and *per capita* abandonment of unprocessed coconuts by different age-classes of the Temple Run group during March 2019–February 2020. Overall comparison of *per capita* use of processed coconuts and *per capita* abandonment of unprocessed coconuts by age-classes are illustrated using violin plots within the graph (inset).

Figure 7. Monthly *per capita* use of processed coconuts and *per capita* abandonment of unprocessed coconuts by different age-classes of the Baywatch group during March 2018–October 2019. Overall comparison of *per capita* use of processed coconuts and *per capita* abandonment of unprocessed coconuts by age-classes are illustrated using violin plots within the graph (inset).

case of early juveniles ($\chi^{2,AC-2}_{Overall,EJ}$=60.80, df=3, p<0.0001) in the second annual cycle alone. In the remaining demographic classes however, no single phenophase of unprocessed coconuts emerged as the single highest. For instance, all phenophases were equally represented among early juveniles in the first annual cycle ($\chi^{2,AC-1}_{Overall,EJ}$=8.00, df=3, p=0.046); P1 and P3 were comparable in the first annual cycle ($\chi^{2,AC-1}_{P1=P3}$=7.06, df=1, p=0.07), and P1 and P2 were comparable in the second annual cycle ($\chi^{2,AC-2}_{P1=P2}$=5.72, df=1, p=0.13) among late juveniles

and almost all phenophases were equivalently left unprocessed by adults in both annual cycles ($\chi^{2,AC-1}_{Overall,AD}$=5.78, df=3, p=0.12; $\chi^{2,AC-2}_{Overall,AD}$=17.20, df=3, p=0.0006). It is interesting to note that P5 coconuts occurred in noticeable proportions (EJ[AC-1]=12.5%, LJ[AC-1]=5.1%, AD[AC-1]=9.5%; EJ[AC-2]=0%, LJ[AC-2]=2.9%, AD[AC-2]=8.8%) across all demographic classes in both annual cycles except in the case of early juveniles in the second annual cycle.

Age-class specific monthly use of processed coconuts and abandonment of unprocessed coconuts by Temple

Table 1. Results of the generalized linear mixed effects model with number of processed coconuts consumed as the dependent variable, month as the random factor and age-class, group identity and sex as the fixed factors. To control for number of individuals in an age-class, we have used an offset term, log (number of individuals). Model fitting has used maximum likelihood method along with Laplace approximation.

Coefficient	Estimate (β)	SE	Z	p
Processed coconuts~ Age class * Sex + Age Class*Group + (1 |Month)				
Intercept	0.268	0.097	2.762	0.0058
Early juvenile	-1.739	0.097	-17.89	<0.0001
Late juvenile	0.221	0.042	5.26	<0.0001
Male	0.218	0.050	4.40	<0.0001
Temple Run	-1.243	0.075	-16.54	<0.0001
Early juvenile: Male	0.520	0.118	4.40	<0.0001
Late juvenile: Male	-0.198	0.067	-2.94	0.0032
Early juvenile: Temple Run	-0.516	0.217	-2.375	0.0175
Late juvenile: Temple Run	0.752	0.088	8.20	<0.0001

*Adult (Age class), Female (Sex class) and Baywatch (Group) have been used as reference categories

Run group

Over and above annual trends, we were interested in monthly patterns of coconut use and coconut abandonment by demographic classes of the two groups while controlling for class size, i.e., number of individuals in a demographic class leading to the computation of *per capita* figures. We present the results of the two groups, TR and BW, in separate sections followed by comparisons of the two groups in the final section. All comparisons use *per capita* values.

Considering a single annual cycle, while early juveniles and adults in TR showed a stable use of processed coconuts across months (KW_{EJ}^{TR}=24.22, *p*=0.01, no difference between months on Dunn's correction for multiple comparison; KW_{AD}^{TR}=8.95, *p*=0.63), late juveniles showed a minor inter-month difference (F_{EJ}^{TR} (11,64) =2.17, *p*=0.03; $\mu_{Sep-2019}$>$\mu_{Mar-2019}$) (Figure 6). As a result of an almost constant use of processed coconut across months and perhaps, lack of greater temporal coverage, no seasonality was observed in the use of processed coconuts by any of the demographic classes. At the level of individual month, we found near-consistent difference between early juveniles and late juveniles but no difference between late juveniles and adults (Figure 6). In contrast, pooling the data through the entire annual cycle showed a distinct demographic pattern with LJ>AD>EJ ($F_{Overall}^{TR}$=112.50, *p*<0.0001) (Figure 6 inset). Similar to the analyses of processed coconuts, we found no variation in the number of coconuts left unprocessed by the demographic classes across months (KW_{EJ}^{TR}=9.99, *p*=0.53; KW_{LJ}^{TR}=21.66, *p*=0.03, no difference between months on Dunn's correction for multiple comparison; KW_{AD}^{TR}=19.18, *p*=0.06; Figure 6)

though across five of the 12 months, there were minor differences across age-classes within a month in which late juveniles emerged as the highest contributor to *per capita* abandonment of coconuts. Consistent with our hypothesis, the following order of coconuts left unprocessed emerged when data for the entire study were pooled together, LJ>AD=EJ ($Friedman_{Overall}^{TR}$=68.62, *p*<0.0001; ΣRank$_{AD}$-ΣRank$_{EJ}$=16.5, p=0.053) (Figure 6 inset). Expectedly, results from generalized linear mixed modeling approach to determine relative influence of the three demographic classes on use of processed and desertion of unprocessed coconuts showed that late juveniles exerted greatest influence followed by adults and early juveniles after controlling for variations due to month and number of individuals within a demographic class (Table 1).

Age-class specific monthly use of processed and abandonment of unprocessed coconuts by Baywatch

On comparing individual demographic classes in their use of processed coconuts across months, we found both, early juveniles (KW_{EJ}^{BW}=66.62, *p*<0.0001) and adults to have unequal use (F_{EJ}^{BW}=5.99, *p*<0.0001) though late juveniles showed a constant consumption pattern (KW_{EJ}^{BW}=41.98, *p*=0.002; No difference between months on Dunn's correction for multiple comparison) across the 20 months of the study. As a consequence, no seasonality in the processing of coconuts was revealed in any demographic class. Next, we attempted to contrast the demographic classes at the level of individual months. The differences among the age-classes appeared to be more subtle than TR since 11 out of the 20 months did not record any difference among the age-classes. Even among months (N_{EJ}=7)
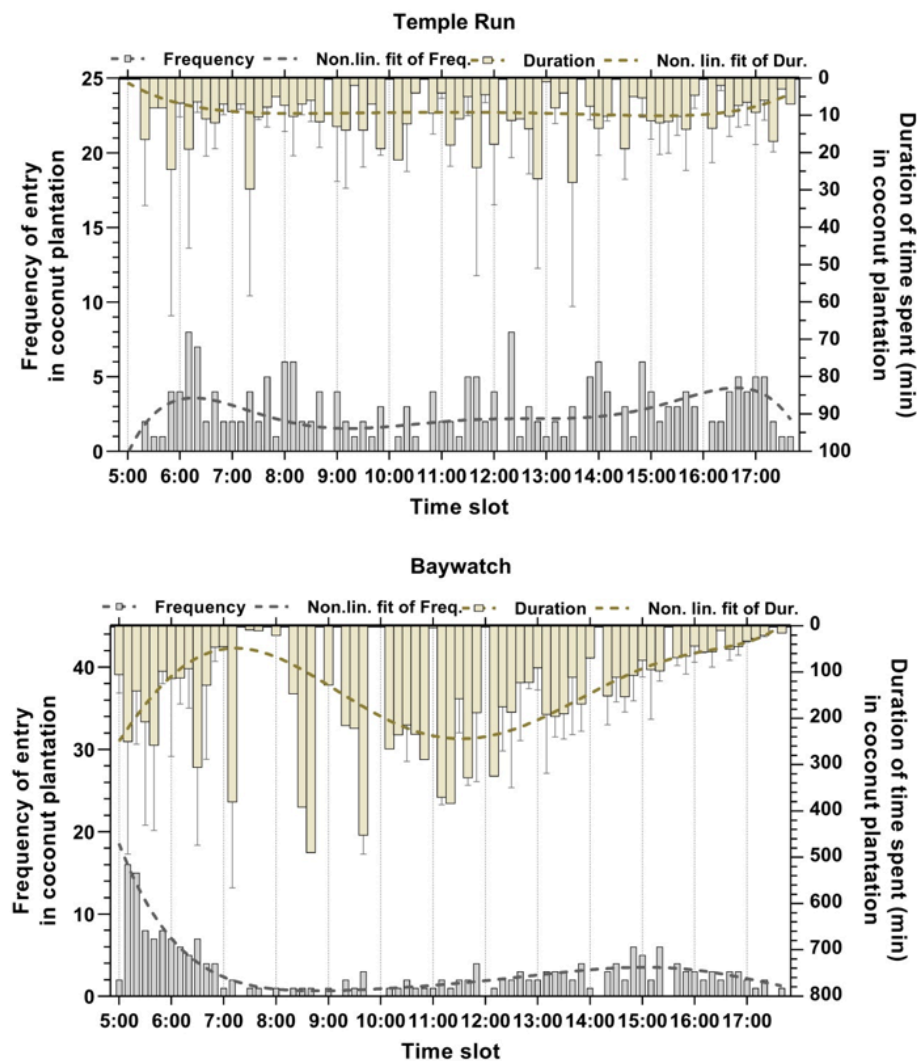
Figure 8. Illustration of 'frequency of entry' and corresponding 'duration of time spent' in coconut palm plantations by Temple Run group (top) and by Baywatch group (bottom). Additional features in the graph include polynomial regression curves to depict trends of distributions shown as dotted lines. Note that the scales of the Y1 and Y2-axes of the two graphs are different.

where difference among age-classes were retrieved, early juveniles emerged to have the lowest *per capita* coconut processing value. Pooling data from the 20 months of observation, we firmly established early juveniles to have the lowest use of processed coconuts (μ_{EJ}±SD=1.12±0.95) but late juveniles (μ_{LJ}±SD=2.24±1.41) and adults (μ_{AD}±SD=2.45±1.58) had almost equal use of processed coconuts leading to the following order of consumption, LJ~AD>EJ ($\text{Friedman}_{\text{Overall}}^{\text{BW}}$=107.10, p<0.0001; ΣRank_{AD}-ΣRank_{LJ}=33.0, p=0.054). A distinct difference among the three demographic classes in BW was revealed with generalized linear mixed model wherein, late juveniles emerged to exert greater influence on overall use of processed coconuts than the remaining age classes (Table 1).

We analyzed data on unprocessed coconuts by demographic classes in a manner similar to processed coconuts. Late juveniles did not vary in abandonment of unprocessed coconuts across months ($\text{KW}_{LJ}^{\text{BW}}$=48.59, p=0.0002; No difference between months on Dunn's correction for multiple comparison) though early juveniles ($\text{KW}_{EJ}^{\text{BW}}$=45.58, p=0.0006) and adults did ($\text{KW}_{AD}^{\text{BW}}$=58.54, p<0.0001) (Figure 7). When demographic classes were compared during each individual month, we found no difference among age-classes during 11 months; at least one difference in paired comparison of age-classes in seven months and just two months during which late juveniles superseded both age-classes (March 2018 and December 2018). Considering overall aggregate figures of unprocessed coconuts discarded by each demographic class, our result matched the trend obtained for processed coconuts, AD=LJ>EJ (

Table 2. Results of the generalized linear mixed effects model with number of unprocessed coconuts consumed as the dependent variable, month as the random factor and age-class, group identity and sex as the fixed factors. To control for number of individuals in an age-class, we have used an offset term, log (number of individuals). Model fitting has used maximum likelihood method along with Laplace approximation.

Coefficient	Estimate (β)	SE	Z	p
Unprocessed coconuts ~ Age Class*Group + (1 |Month)				
Intercept	-2.293	0.113	-20.259	<0.0001
Early juvenile	-0.577	0.137	-4.206	<0.001
Late juvenile	1.152	0.090	12.768	<0.0001
Temple Run	-0.338	0.203	-1.662	0.0966
Early juvenile: Temple Run	0.070	0.369	0.189	0.850
Late juvenile: Temple Run	0.767	0.217	3.528	<0.001

*Adult (Age class) and Baywatch (Group) have been used as reference categories

$\text{Friedman}_{\text{Overall}}^{\text{BW}}$=107.10, p<0.0001; ΣRank$_{\text{AD}}$-ΣRank$_{\text{LJ}}$=7.0, p>0.99) (Figure 7 inset). Although, macaques of both troops avoided heavily defended regions of palm plantations, we did not find any difference in the number of coconuts left unprocessed among high (HR), moderate (MR) and low risk (LR) areas of coconut plantations($\chi_{\text{HR}\sim\text{MR}}^{2,\text{TR}}$=2.51, p=0.54; $\chi_{\text{HR}\sim\text{LR}}^{2,\text{TR}}$=3.21, p=0.33; $\chi_{\text{HR}\sim\text{MR}}^{2,\text{BW}}$=0.01, p=0.99; $\chi_{\text{HR}\sim\text{LR}}^{2,\text{BW}}$=4.15, p=0.13).

The results of the generalized linear mixed effects model considering processed coconuts from both groups revealed that males superseded females by a mean difference of 0.22 in *per capita* coconut consumption after adjusting for age-class. We also found late juveniles to have an overall highest mean *per capita* use of processed coconuts followed by adults and early juveniles (Table 1) despite late juveniles in BW consuming an equivalent number of coconuts as adults in BW. Among other comparisons, BW and each representative age-class of BW had higher mean *per capita* use of processed coconuts than TR and its corresponding age-classes (Table 1). In contrast, when unprocessed coconuts from both groups were pooled, BW and TR were comparable along with early juveniles of both the troops (Table 2). Comparing age-classes of the two groups in their abandonment of unprocessed coconuts, we found that adults of BW superseded adults of TR and conversely, late juveniles of TR surpassed late juveniles of BW. In addition, an overall age-class related differences persisted where the mean difference in *per capita* abandonment of coconut processing between LJ and AD, and between EJ and AD were 1.15 and 0.58, respectively (Table 2).

Hourly pattern of entry into coconut plantations and corresponding duration of foray by Temple Run and Baywatch groups

Temple Run exhibited a low but an approximately uniform frequency of entry (~2–3 entries every 10 minutes) into plantations throughout the day with minor peaks appearing at ~06.30h and at ~16.45h. An analogous trend was obtained in pattern of duration of time spent which rose from an average of 0 min at 05.00h to 4 min at 06.00h and remained at an average of 10 min till ~17.00h before declining to 0 min.

Unlike the trends of foray duration obtained in TR, BW began their entry into plantation slightly early and at a frequency of 16 (if the initial frequency of 2 at 05.00h is ignored) at 05.10h after which, the trend of entry declined sharply till 07.50h to null. Frequency of entry gradually picked up to 6 till 14.50h and gradually fell to null again at ~17.30h. Although similar in form but widely different in magnitude, BW spent more time in coconut plantations between roughly 09.30–13.30 h with peak average duration reaching 250 minutes (as estimated from the polynomial trend line). Average duration of foray into plantation at the tail of the trend line showed an asymptotic relationship with the straight line slope of one (θ=45°) due to the constraint of activity period of the species.

DISCUSSION

In the first part of our article (Das et al. 2020), we applied the HIREC framework to study differential use of coconut palms and palm plantations by a wide variety of groups of long-tailed macaques differing in their exposure to coconut and thus, to agricultural landscapes, habitat alterations and to biotic threats from crop defending dogs/humans. In the present article, we extended the HIREC framework to study the response of demographic classes and decompose the use and abandonment of coconuts. We found

late juveniles to consume and abandon the highest number of coconuts across annual cycles. On overall comparison by pooling data from both groups, males emerged to use a higher share of processed coconuts than females though sex-difference reversed in the late juvenile age class. Due to a skewed sex ratio (TR=1:4, BW=2:14) in the adults, sex differences in the use of processed coconuts should be interpreted with caution. Early juveniles constrained by their physiology and limited processing repertoire almost exclusively used P1 coconuts though with maturity, individuals used higher phenophases of coconuts. Adult individuals were found to equalize their choice of coconuts across phenophases than late juveniles. The MVT construct predicts patch-usage and patch-leaving decisions (e.g., Wajnberg et al. 2000). Similar to results obtained in the first part of the article (Das et al. 2020), entry into coconut plantations were slightly more frequent during dawn and dusk though usage of plantation remained stable through the day. Temple Run showed a uniform frequency of use of coconut clusters/plantations through the day but BW showed temporal modulations. The corresponding profile of the distribution of 'duration of foray' between the two groups, however, was highly variable. The two groups also differed with regard to the spatial proximities of their respective sleeping sites to nearest coconut plantations. Temple Run consistently chose sites that were slightly aloof from human habitations and hence, distant from palm plantations. On the other hand, Baywatch had six of a potential eight sleeping sites within 100m from palm plantations with three of them located inside less-disturbed (i.e., low risk) regions of the plantations. As a result of a relatively wider (though sparse) distribution of coconut palm occurring within the range of TR, they accessed coconut throughout the day in contrast to BW.

Age-specific use of processed coconuts and abandonment of unprocessed coconuts by Temple Run group in a single annual cycle and by Baywatch group in two consecutive annual cycles

The pattern of age-class governed unprocessed coconuts mirrored the trend of processed coconuts. Dynamics of the un-standardized age-class recorded in the dataset of BW, however, showed less consumption of coconuts by late juveniles than adults due to a much smaller count of late juveniles and as a result of stable demographic structure, the trend remained constant over annual cycle. The disproportionately high records of unprocessed coconuts abandoned by late juveniles relative to other age-classes reflects indiscriminate and perhaps, naïve acquisition/plucking of coconuts since a

large subset is often unsuitable for consumption with coconut abandonment, emerging as a byproduct of pedagogic explorations of coconut. As is apparent, such explorative tendencies are limited to young juveniles, since they are physiologically/cognitively/mechanically constrained but not in adults as they have the requisite cognitive and motor skills to harvest desired coconuts. In support of age-related proficiency of food processing, description of cashew (*Anacardium* spp.) processing by Wild Bearded Capuchins *Sapajus libidinosus* also found age to be a strong predictor of success in opening fresh and dry forms of the nut (Visalberghi et al. 2016).

Use of different phenophases of processed coconuts by Baywatch group expressed as overall proportions and as demographic class-specific proportions across two annual cycles

The frequency of use of phenophases of processed coconuts followed the developmental order of phenophases with the most immature stage(s) of coconut being used by all age-classes over all the subsequent phases of coconut. The share of P2 and P3/P4 phenophases in the diet of early juveniles were meager and records were made only from the oldest individuals in the category. Conversely, higher age-classes had greater representations in mature phenophases of coconuts with adults displaying skilled use of tougher/harder coconuts than late juveniles. A study by Schaik & Noordwijk (1985) on Sumatran Long-tailed Macaques also found adult males to select native wild fruits with hard rinds relative to juveniles of <2 yrs. In contrast, Visalberghi et al. (2016) found that adult females process a higher number of both dry and fresh cashews. Analyses of the relative use of different phenophases of coconuts within individual age-category clearly expounded age-related patterns of resource use which denote a strong ontogenetic effect on extractive foraging of coconuts. Similarly, balance and optimality in choice of phenophases also seem to be achieved at adulthood.

Abandonment of different phenophases of coconuts (unprocessed) by Baywatch group expressed as overall proportions and as demographic class-specific proportions

The trend of age-related unprocessed coconuts was incoherent across annual feeding cycles, however, age-class with the highest explorative tendencies was found responsible for the highest number of unprocessed coconuts. It is intriguing to note that despite being incapable to process P4 and P5 coconuts, early juveniles proactively made efforts to dislodge and dehusk these coconuts. For the remaining age-classes, incidences of

unprocessed coconuts were almost uniformly distributed across the phenophases with P1-P3 showing highest incidences among late juveniles in the first annual cycle and P1-P2 occurring in higher numbers in the second annual cycle. Curiously, despite their proficiencies in coconut processing, even adults showed a substantial abandonment of P5 coconuts.

Age-class specific per capita use of processed and abandonment of unprocessed coconuts by Temple Run and Baywatch groups across months

Representation of the monthly use of processed coconuts and abandonment of unprocessed coconuts by age-classes distinctly identified late juveniles to supersede the remaining age-classes though a slight difference was noted in the month with the highest average *per capita* use/un-use (September in TR and August in BW; similar to overall coconut consumption in Das et al. (2020)). Analyses of pooled data from the entire study period in the two troops reaffirmed the distinction of late juveniles in TR though late juveniles were marginally comparable to adult females in use of processed coconuts. The difference in the results of the two groups is attributable to the disparity in their food habits. As opposed to the natural diet of BW, TR has a considerable dependence on human-cultivated and artificially manufactured food items (Das et al. 2020). Late juveniles displayed adult-like use of coconuts and developed commensurate sensorimotor and cognitive skills requisite for extractive foraging, a direct evidence of high dietary dependence on the drupe. Similar to Long-tailed Macaque, Wild Bearded Capuchins were also found to show age-specific hierarchy in average *per capita* processing of fresh cashew nuts. Adults and late juveniles processed equal number of dry cashew nuts on an average (Visalberghi et al. 2016). Remarkably, the seasonality in the overall use of processed coconuts noted in Das et al. (2020) failed to prevail when consumption was decomposed into age-classes. The absence of seasonality in coconut-use by age-classes prompts us to speculate that as a consequence of coconut scavenging, i.e., feeding kernel and/or drinking water from an already processed coconut, cumulative harvest can satiate the entire group. Males consumed higher coconuts in all age-classes, except in late juvenile stage possibly, as a result of dimorphism in body sizes, which either, indicates non-coconut resource use by females or that body-size maintenance by adult males trump energy requirements of reproduction in females. Consistent with the trend of crude comparisons of abandoned unprocessed coconuts by age-classes, late juveniles had the highest overall *per capita* contributions

to unprocessed coconuts, especially in TR. Despite lower use and hence, lower dependence on coconuts by late juveniles in TR relative to their counterparts in BW, late juveniles in TR showed significantly higher abandonment of coconuts indicating inefficacious handling and/or selection of coconuts, an indication of suboptimal coconut foraging/processing strategy. It is also to be noted that coconuts left unprocessed can often be processed by the same or a different individual and hence, is not a veritable index of crop loss.

Hourly pattern of entry into coconut plantations and corresponding duration of foray by Temple Run and Baywatch groups

Temporal profile of entries to plantations and duration of forays were largely modulated by the spatial distribution of coconut palms within the range of groups. BW appeared to prefer coconuts as their first choice of food at the beginning of the day, strategically choosing sleeping sites that were either adjacent to or inside palm plantations. Correspondingly, the distribution of time spent in the morning during the first phase foray was very high and coincided with the first foraging bout. Forays into plantations later in the morning (i.e., after 07.20h) tended to be shorter than forays undertaken earlier (i.e., around 05.20h), possibly because sources of hydration and/or food has been accessed. Subsequent use of plantations through the day remained relatively low gradually increasing after 12.30h and peaking at 15.30h, which corresponds to evening bouts of foraging. As a result of the edge distribution of the plantations within the home range of the group, duration of time spent in mid-afternoon tended to be longer as suitable foraging patches were distantly located from the range edge. Patch-exit decisions by BW were sporadically coerced by threats from humans/dogs guarding the plantations, creating a landscape of fear that groups responded to even in the absence of threat (Lindshield 2014; Gallagher et al. 2017). For instance, arboreal paths were preferred to enter risky areas of the plantation and nervous terrestrial locomotion were noted among the most vulnerable members of the group as is often reported in crop-foraging populations of non-human primates (e.g., Long-tailed macaques, Riley & Priston 2010; Chimpanzee, Krief et al. 2014). The second group, TR on the other hand had access to relatively uniform distribution of coconut palms/clusters throughout its home range and therefore, entered/exited clusters regularly throughout the day spending almost equivalent duration throughout the day. Hostilities, however, did not have any effect on proportion of coconuts abandoned in riskier human areas. The lack of sharp

peaks in the temporal distribution of plantation entry could also be a strategy in response to anthropogenic hostilities faced there. By flattening the temporal curve of plantation entry through the day, the probability of occurring in plantations through the day although low, becomes finite and hence, possibility of facing resistance becomes low. Therefore, alongside physiological (like hunger and thirst) and resource-based (like abundance, distribution and nutrition) factors, spatiotemporal pattern of threat from human/dog modulates resource patch usage. Applying the HIREC-MVT construct, we infer that coconuts are highly energetic sources of food and nutrition for the species and are lucrative enough to risk entry into moderately-defended portions of plantations. Selective pressures of this human-macaque interface especially, for an edge population has also prompted the development of surreptitious foraging tactics in both the groups, exemplified by suppression of vocal communication, heightened vigilance, spurts of rapid movements and controlled motor actions to reduce noise.

To summarize, extractive foraging of an embedded and heavily-defended cultivar, like coconut have challenged macaques in many ways. For example, the embedded/encased nature of the fruit permits early juveniles to exploit only tender phenophases of coconuts. Adults face similar hurdles with mature stages of coconuts and hence have a balanced choice of phenophases that optimizes net benefits. Even context-specific choice of phenophases by adults though not explored in this article is suspected, which could further elucidate cognitive proficiencies of adults in determining suitability of coconut. It is remarkable to note that description of the use of a single dietary resource generated the order of consumption precisely as predicted by the theory of life-history strategies. A second class of challenge emanates from coconut foraging from highly defended plantations, which is studied by describing temporal strategies of plantation entry and plantation use. The groups were found to employ deceptive strategies suited to minimize detection by maintaining the probability of entry to plantations at a non-zero level through the day and by adopting covert communications and clandestine movements inside plantations, a subject matter that we will further explore.

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