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Skills, Division of Labor, and Economies of Scale Among Amazonian Hunters and South Indian Honey Collectors

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Abstract

In foraging and other productive activities, individuals make choices regarding whether and with whom to cooperate, and in what capacities. The size and composition of cooperative groups can be understood as a self-organized outcome of these choices, which are made under local ecological and social constraints. This article describes a theoretical framework for explaining the size and composition of foraging groups based on three principles: (1) the sexual division of labor; (2) the intergenerational division of labor; and (3) economies of scale in production. We test predictions from the theory with data from two field contexts: Tsimane' game hunters of lowland Bolivia, and Jenu Kuruba honey collectors of South India. In each case, we estimate the impacts of group size and individual group members' effort on group success. We characterize differences in the skill requirements of different foraging activities, and show that individuals participate more frequently in activities in which they are more efficient. We evaluate returns to scale across different resource types, and observe higher returns at larger group sizes in foraging activities (such as hunting large game) that benefit from coordinated and complementary roles. These results inform us that the foraging group size and composition are guided by the motivated choice of individuals on the basis of relative efficiency, benefits of cooperation, opportunity costs, and other social considerations.

Keywords: economic specialization, sexual division of labor, intergenerational division of labor, returns to scale, optimal group size, hunting and gathering.

Introduction

Cooperation and collective action are hallmarks of human societies and major foci of research in the evolutionary sciences [1,2]. Cooperation in food acquisition and sharing of food resources are particularly critical features of foraging economies [3], whose relevance for understanding the course of hominin evolution is well acknowledged [4]. While cooperation appears to be universal and important to success in human societies that practice foraging, and perhaps in all human societies, the nature and scope of cooperation is quite variable within and among groups.

Much of the variation in the size and composition of groups that forage for wild resources appears to be patterned with respect to social and ecological environments. Examples of these patterns of variation are abundant in the ethnographic literature. For example, Steward reported that Shoshoni hunter---gatherers of the U.S. Great Basin hunted solitarily

during winter months and families were largely self---sufficient, but aggregated in larger groups and participated in communal game drives during the summer [5]. Among the Ache of Paraguay, armadillos and deer are hunted solitarily, while cooperative groups form to pursue white---lipped peccaries, monkeys, coatimundis, and spotted paca [6–8]. While women are often involved in cooperative pursuits of coatimundis, they rarely participate in pursuits of other animals. In cooperative paca hunts, the role of flushing the animal is given to younger, less skilled hunters, while the role of killing the animal by hand is allocated to older, more skilled hunters. Among Lamalera whale hunters, roles within large cooperative parties and the distributions of rewards depend on age, kinship, and boat ownership in complex ways [9].

The goal of this paper is to provide a theoretical framework for explaining the size and composition of groups engaged in foraging activities, and to test a series of hypotheses derived from the framework. These principles build on previous work in economics and ecological anthropology, focusing attention on maximizing group efficiency when group members actively pool the spoils of labor [10–12]. We propose that three fundamental features of human foraging economies interact in generating patterns of cooperation in foraging groups, and more generally in most human societies.

The first feature derives from the differential risks and gains for women and men from engaging in different economic activities [12–17]. Productive activities that present a significant danger of injury, such as hunting mobile prey, are likely to generate particularly high gains to a sexual division of labor. Because of the intensive childcare practiced by human mothers, hunting by women engaged in childcare would expose infants to substantial risks. Infants may also encumber movement and lower return rates. While women may be fully capable of developing the skills necessary to hunt successfully, the inability to build up experience while pregnant and nursing results in differences in productivity based on skill [15]. We propose, as have others, that the nutritional value of meat interacting with differential costs of hunting for the two sexes leads to a sexual division of labor with subsequent sharing of resources and biparental investment within families [11–14]. Other resources, such as honey produced by stinging bees high in trees, also generate differential risks for men versus women engaged in childcare. With this type of specialized coordination, the sexual division of labor in subsistence will be organized by factors generating differential risks and benefits for females and males based on the skills required for production. (Other factors, such as local gender norms and expectations, may either mediate or interact with the effects of these constraints, as we discuss below.)

The second feature affecting patterns of production in foraging economies is that the resources acquired demand substantial levels of accumulated skill. Studies from a variety of foraging contexts show that foragers do not reach peak economic efficiency until middle adulthood (usually in the 30s or 40s), and that peak efficiency is achieved later in life for resources requiring greater levels of skill [18–24]. We hypothesize that variation in skill and strength requirements for different resources generates an age--- structured division of labor in foraging groups that complements the sexual division of labor [11]. The intergenerational division of labor is associated with a flow of resources between generations based on kinship. Net transfers (amount given minus amount received) tend to be directed downward from older to younger individuals with three---generations participating: grandparents, their adult children, and grandchildren [25,26]. Children and adolescents tend to not participate in skill---intensive, strength---intensive, or dangerous subsistence activities; they work less than adults and focus on learning and producing resources that are easily acquired [27–29].

A third principle organizing cooperation in foraging is economies of scale with respect to the number of individuals in a production group [10,30–34]. Foraged resources vary in terms of the relationship between the number of individuals in the foraging party and the amount acquired. For some resources, solitary individuals may be capable of achieving near---maximal return rates. Return rates from other resources may increase significantly as more individuals are added to the pursuit group. We propose that where individuals can voluntarily assort themselves, and in the absence of other external constraints, foraging parties will tend to form that maximize *per capita* expected returns. When these conditions hold, variation in the size of parties will reflect ecological variation in economies of scale. Economies of scale derive principally from features of the resource, the technologies used in its acquisition, and the social institutions that shape the rules of joint production and/or distribution. Some mobile resources are more easily captured when several individuals cooperate, for example by blocking escape routes, herding animals, or by following specific individuals as groups disperse [8]. In general, hunting large and group---living animals often exhibits economies of scale. Collected foods, such as honey produced and defended by stinging bees, may also exhibit economies of scale involving a coordinated division of roles. Within societies, under conditions of voluntary assortment, the size of foraging parties should reflect differences in economies of scale among the specific resources or suites of resources being targeted. Variation among societies is expected to reflect the quantitative mix of resources they pursue.

Our proposal is that the interaction of those three principles—the division of labor by sex, the division of labor by age, and economies of scale—can help explain the size and composition of foraging groups. As a first step in assessing the relevance of these principles we test a series of hypotheses in two societies, Tsimane' forager---horticulturalists of lowland Bolivia, and Jenu Kuruba honey collectors of South India, focusing on two different types of foraged resources: hunted meat and collected honey. These two societies were selected given that both actively engage in foraging in addition to other economic pursuits, and extensive data on the size and composition of foraging parties permit a parallel series of statistical tests. In each case, we test hypotheses about the efficiency of individuals and groups in foraging, then test corollary hypotheses regarding the size and composition of the groups themselves.

The analysis of foraging efficiency utilizes an estimation strategy developed in econometrics and utilized with increasing frequency in quantitative anthropology [30,31,35]. This strategy estimates the effect of inputs to production—in this case, the number of individuals or hours contributed by individuals of a given age and sex—on total group production in terms of the *elasticity of production with respect to each input*. The elasticity represents the expected percent change in output associated with a percent increase in the input. Elasticity values close to 1 indicate that a one percent increase in the input result in an equal percent increase in production (i.e. constant returns to scale), while values greater than or less than 1 indicate increasing or decreasing returns to scale, respectively. (Further details regarding this estimation strategy and its interpretation are described in ESM Section 1.) The following three hypotheses will be tested regarding the <u>efficiency of individuals of foraging groups</u>:

> H1: The efficiency of males will be greater than that of females in skill--- or strength---intensive foraging tasks that are incompatible with childcare.

- P1: The elasticity of production with respect to male participation will be higher than the elasticity of production with respect to female participation.
- P2: The elasticity of production with respect to male labor (in terms of time effort) will be greater than the elasticity of production with respect to female labor.
- P3: The difference in the elasticities with respect to male and female inputs will be greater for larger game species and for more skill--- or strength---intensive tasks.

> H2: Efficiency in skill---intensive foraging activities will be greatest at middle and older ages due to the importance of experience and learning.

- P4: The elasticity of production with respect to the participation of middle---aged and older adult males will be higher than that of younger males.
- P5: The elasticity of production with respect to the labor of middle---aged and older adult males will be higher than that of younger males.
- P6: The difference in the elasticities with respect to the inputs of younger versus older males will be greater for larger game species and for more skill--- or strength---intensive activities.

> H3: Individuals will perform specific roles within foraging parties in which they are more efficient in accordance with H1 and H2.

- P7: Older males will perform more dangerous, skill---intensive, and strength---intensive tasks more often than females or younger males.

The following five hypotheses will be tested regarding the <u>size and composition of foraging parties</u>:

> H4: Individuals will tend to participate in foraging parties in which they are relatively more efficient, in accordance with H1 and H2.

- P8: Females will participate in foraging parties less often than males.
- P9: Middle---aged and older males will participate in foraging parties more often than younger males.

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H5: Parties engaged in foraging activities that require more specialized skills will be composed more exclusively of individuals possessing those skills.

- P10: Heterogeneity in the age and sex of participants will be lower for larger game and more skill- -- or strength---intensive activities.

H6: For activities regularly undertaken in groups, the productivity of the group will be characterized either by constant or increasing returns to scale with respect to the participation and labor of group members.

- P11: Per capita returns will remain constant or increase with additional participants (particularly men) in foraging groups.[1]

H7: The party sizes that maximize per capita efficiency will vary according to the type of resource pursued.

- P12: The impact of additional group members on per capita returns will be greater for species requiring multiple coordinated or complementary roles (particularly for larger, group---living, and more dangerous species).

H8: The size of parties pursuing a given resources will reflect returns to scale in the production of that resource.

- P13: The mean size of foraging parties will be greater for those species identified in P12.

This set of hypotheses is derived from the specific principles outlined above, but is not meant to account for the totality of reality on the ground. When empirical results do not conform to a framework focused on group efficiency, we are stimulated to develop alternative hypotheses. In the discussion that follows, we address the current results in light of hypotheses emphasizing other social benefits and constraints, such as learning, social norms, and failures of coordination and cooperation [10,36–38]. These data are also observational, based on the size and composition of parties observed over a limited timespan, while individual efficiencies depend on endogenous decisions made over the course of life. We are therefore limited in our ability to make inferences about all processes that affect group formation. Analysis of the variation in observed patterns can nonetheless shed important light on the efficiencies that stem from individual choices.

The rest of the paper is organized as follows. In the next section, we provide an ethnographic overview and a description of the economies of the two societies from which the data are derived. We then report the results of the analysis of the Tsimane' and Jenu Kuruba data in sequence. We conclude with a discussion of the extent to which the data support the hypotheses, and future directions for assessing the generalizability of the proposed framework.

Study Sites and Methods

A. Tsimane' Study Site

The Tsimane' are an indigenous Amerindian population residing in the Beni Department of lowland Bolivia (pop. ~12,000 in 2010). The majority (96%) of the Tsimane' diet derives from subsistence production in the form of swidden horticulture (66%), hunting (17%), fishing (7%), and collecting fruits and nuts (6%) [39]. Some families earn income from selling horticultural products (principally rice) and from wage labor with Spanish---speaking ranchers and loggers. Tsimane' hunters travel in the forest in search of game solitarily or in groups, and subdue prey using shotguns, 0.22---caliber rifles, bows and arrows, machetes, axes, sticks, or bare hands [19].

The hunting data employed in this analysis were collected between 2005 and 2010 by PH, MG, HK, and other members of the Tsimane' Health and Life History Project. Production---and---sharing interviews were conducted by research assistants in the Tsimane' language with 245 nuclear families in eight communities twice weekly over an average of

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[1] Where increasing returns to scale are expected but not observed, assumptions of classic foraging models (e.g. complete)

14 months in each community. (For further details on the interview sample and methods see [20,25].) For each family member that was reported spending time hunting in the preceding two days, the number of hours spent hunting, whether attention was divided between hunting and fishing, and the identities of all individuals in the hunting party were recorded. Individuals that were reported hunting together on the same day were considered to be members of the same hunting party. For each prey animal obtained, the species, the identity of the individual(s) who encountered and killed the prey, and the method of killing were recorded. The mass and caloric values for each game species were derived from field measurements and South American nutritional tables [40,41].

The production---and---sharing interview dataset yielded a total of 3201 unique hunting parties, ranging in size from 1 to 7 individuals. 266 hunting parties in which attention was split between hunting and fishing were excluded from the analysis, as the relative proportion of time devoted to each task was unknown. 47 species of prey were obtained, predominantly collared peccary, coatimundi, paca, deer, armadillo, tapir, and a variety of monkeys, birds, and turtles. For the most fine---grained analysis, prey were grouped into 7 non---overlapping categories: (1) large mammals (over 12 kg) excluding peccary and deer; (2) peccary; (3) deer; (4) monkeys; (5) small mammals (under 12 kg) excluding monkeys; (6) birds; and (7) turtles. For more coarse---grained analyses, prey were grouped into 3 categories: (1) peccary and other large mammals excluding deer ("large mammals"); (2) deer and monkeys; and (3) small mammals (excluding monkeys), birds, and turtles ("small game"). Individual credit for producing game was divided evenly between the individuals that were credited for encountering and killing the prey.

B. Jenu Kuruba Study Site

The Jenu Kuruba are an indigenous *adivasi* ("First Dweller") population living in the Western Ghats in South India, primarily in the state of Karnataka, where they number about 30,000 [42]. Around the area of Kodagu, many Jenu Kuruba live in the dry deciduous tropical forest, where they complement household cultivation and wage labor on local coffee estates with seasonal collection of forest produce, including wild honey. KD worked in a cluster of five villages located 1---3km inside the Reserve Forest. About 500 people live in these villages and have the right to collect honey for consumption and sale.

Four types of wild honeybees migrate to Kodagu just before the monsoons in May and November. Individuals collect honey from all four types of bees, but only the two largest produce honey in sufficient quantities to turn a reliable profit. The giant Asian honeybee, known locally as hejjenu (*A. dorsata*), makes exposed combs that hang high in trees from sturdy branches. Honey collectors must climb up to the combs, use smoky torches to pacify the bees, then lower the honey to the ground with the aid of baskets.

Jenu Kuruba report that this is best accomplished in groups of at least three people to allow a division of labor. Giant Asian bee combs can yield up to 30 kilograms of honey, which is sold for 60---80 rupees per kilogram[2]. Collecting from the giant Asian bee is difficult and can be dangerous: three serious falls were reported to KD during 2009. Thuduvejenu (*A. cerana*), a honeybee similar in size and temperament to the western honeybee, can be collected alone or in small groups. Collectors must cut into the tree cavity or termite mound to expose the hive and carefully remove the combs. Smoke from a cigarette is often used to subdue the bees. Hives yield 1---10 kilograms of honey, which is sold for ~100 rupees per kilogram.

Hives are not privately owned, so when possible, the location and size of western---sized bee hives are kept secret. The two other honeybees, koljenu (*A. florea*) and nasarajenu (*Trigona spp.*), are both very small (<1 cm), stingless bees that make tiny honey combs in cavities of branches or bamboo. Children often practice honey collecting with these species. These two stingless species have been lumped together in this analysis given their similarity. See [21,43] for a detailed treatments of Jenu Kuruba honey collecting and the acquisition of honey collecting skills across the life cycle.

KD spent nine months during 2009 in participant and ethnographic observation of Jenu Kuruba honey collecting. A questionnaire eliciting information about an individual's most recent honey collecting event was administered to 90% of males and a random sample of 25% of females in five villages. The current analysis is based on a sample of 109 honey---collecting trips reported by individuals aged 7---70 years old. Information was recorded regarding the number of group members, their sex, their juvenile/adult status (<16 versus ≥16 years old), the type of honey collected, the reporting

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[2] A day's wage labor on a coffee estate is worth 125 rupees for men. In 2009, 50 rupees ≈ 1 USD.

individual's principle role (making smoke, cutting combs, assisting, or observing), and the value from sale of the honey in rupees (perceived to be more accurately recalled than estimates of mass). A lack of double---reporting honey collecting events was inferred from the fact that the composition of each reported group was unique. Skill requirements for honey collecting tasks and bee types were assessed qualitatively through ethnographic observation and discussion with study participants.

Data Analysis Methods

See ESM section 1.

Results

A. Tsimane' Hunting Groups

[Fig. 1 about here]

Fig. 1 presents the results of regression models predicting the caloric productivity of individuals from each day spent hunting as a function of age, sex, and time effort (reported in ESM Table E1). In support of P1, the marginal mean productivity of men from hunting (holding labor constant) exceeds that of women across all ages (Fig. 1a and Table E1 model A). This result holds across three different types of game: peccary and other large mammals (Table E1 model B); deer and monkeys (model C); and small game (including small mammals, birds, and turtles; model D). Consistent with the general incompatibility of childcare with success in hunting, mothers of children aged 0---2 that participated in hunting showed significantly lower productivity (coefficient ---0.43, 95% CIs ---0.85—---0.01; Table E1 model A). In support of P2, the estimated elasticity of individual production with respect to time effort is greater for men than women throughout adulthood (Fig. 1b). P3 predicted that the difference in the productivity of males and females would be greater for larger and more skill---intensive species of game. The breakdown by prey type shows that the differences between the estimated elasticities of production for men versus women are greater for more skill---intensive targets—peccary and other large mammals (Fig. 1c), and deer and monkeys (Fig 1d)—than for less skill---intensive small mammals, birds and turtles (Fig. 1e).

Fig. 1a shows that P4 is supported, in that the marginal mean productivity of older men exceeds that of younger males still in their teens and 20s, and peaks around age 40. Fig. 1b supports P5, showing that the estimated elasticity of production with respect to labor is greater for middle---age and older adult men compared to younger males. Somewhat unexpectedly, given the expected importance of aging for physically---intense activities, the estimated elasticity for males >50 exceeds that of men in middle age (26--- 50). In support of P6, the difference between the elasticities for older men versus younger males is greater for peccary and other large mammals (Fig 1c), and deer and monkeys (Fig 1d) than for smaller, easier game species (Fig. 1e).

[Fig. 2 about here]

The distribution of the sizes of 3201 Tsimane' hunting parties is given in ESM Fig. E1. The mode of this distribution is solitary hunting (2352, 73% of parties). 26% of parties (817) fall in the range of 2—4 individuals, while 1% of parties (32) contain five or more individuals. The composition of parties according to size is given in Fig. 2. Consistent with P8 and P9—which predict that the age---sex class achieving the highest gains and facing the lowest opportunity costs will differentially participate—Fig. 2 shows that adult males are the primary participants in hunting groups, outstripping both females (P8) and adolescent males (P9). The differential probability of hunting is also manifest in ESM Fig. E2 (based on ESM Table E2), which shows that middle---age men are the most likely to hunt on any given sample day (12% probability), followed by young adult and older adult men (6%), adolescent males (1%), and females (≤0.5%). In support of P10, hunting parties capturing large mammals, peccary, deer, and monkeys are composed more exclusively of adult men (Fig. 2a), while females and sub---adult males appear with greater frequency in larger groups targeting smaller and easier---to---capture species (Fig. 2b).

[Fig. 3 about here]

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Fig. 3 displays mean total and per capita production from hunting as a function of the total size of parties (panels a and b) and the number of adult men (the most productive age---sex class identified in Fig. 1; panels c and d). Consistent with P11, total production increases roughly linearly across parties of 1, 2, and 3 individuals, yielding roughly constant per capita production. Per capita returns are noticeably greater in groups of 4 and 5, apparently exceeding expectations of constant returns to scale. Higher per capita returns in larger groups are particularly pronounced when counting the number of adult men in the group (Fig. 3d).

[Fig. 4 about here]

Fig. 4 (based on ESM Table E3) quantifies returns to scale in terms of the elasticity of total group production with respect to the labor of group members. Fig. 4a (Table E3 model A) shows an estimated elasticity for all group members of 1.08 (CIs 0.84—1.31), consistent with roughly constant returns to scale. Fig. 4b recasts the results of Fig. 1 bearing on P1, P2, P4 and P5 in terms of total group (rather than individual) production: middle---aged men show the highest elasticities, followed by young adult and older men, followed by adolescent males and females (Table E3 model B). The estimated elasticity of production with respect to the sum of men's labor is 1.15 (CIs 0.88—1.42; Fig. 4c and Table E3 model D). Table E3 model F estimates the contributions of adult male group size and labor as complementary inputs to production, yielding coefficients of 0.84 (CIs 0.53—1.15) and 0.34 (CIs 0.19—0.49), respectively, suggesting a pattern of greater productivity for each hour spent in larger male groups. This pattern of returns is illustrated in Fig. 4d: due to the complementarity between men's time effort and the number of men, larger groups are predicted to produce both absolutely more at a given effort level, and achieve a higher marginal productivity of effort.

[Fig. 5 about here]

Fig. 3b establishes the relationship between the type of prey captured, total group size, and per capita productivity. In support of P12, per capita productivity from capturing peccary and other large mammals (apart from deer) is maximized in groups of 4 or 5 individuals. Per capita productivity from capturing deer and monkeys, on the other hand—effectively shot by single hunters with rifles from a quiet distance—is near---maximal in parties of 1 or 2 individuals. Per capita productivity from killing small animals is maximal in the smallest (1---person) parties. The mean size of parties by prey type, plotted in Fig. 5, supports P13: parties targeting peccaries and other large mammals tend to be larger than parties targeting deer, monkeys, and smaller prey (see also the histograms of party size by prey type given in ESM Fig. E3). Fig. 5 shows that parties that return without success are significantly smaller those that successfully obtain prey, reflecting a higher probability of success in larger groups.

[Fig. 6 about here]

B. Jenu Kuruba Honey Collecting Groups

Fig. 6 presents regression results estimating the elasticity of total group production as a function of the number of individuals of different age and sex classes in the honey collecting party (from ESM Table E4). Consistent with P1, the elasticity of honey sales with respect to the participation of adult men is exceeds that of women (Fig. 6b). Consistent with P3, only men produce honey from the most skill--- intensive, dangerous, and profitable giant Asian bee. In agreement with P4, the estimated elasticity of production for adult males compared with adolescent males (Fig. 6b).

[Table 1. about here]

The multinomial regression in Table 1 predicts the specific roles played by individuals in collecting honey—making smoke, cutting combs, assisting, or observing—as a function of age and sex. Preparing smoky torches was reported to require the highest level of skill and danger, as torches must produce a continuous, intense stream of smoke for the duration of collection from the giant Asian bee. Consistent with this observation and prediction P7, Table 1 shows that adult males are significantly more likely to prepare smoke than females or younger males. Juvenile males and adult females are both likely to cut combs or assist when they collect honey. Juvenile females primarily observe others during honey collecting events, and are significantly less likely to cut combs.

[Fig. 7 about here]

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ESM Fig. E4 shows the observed distribution of honey collecting party sizes, which range from 1 to 8, with a mode of 1—2 individuals, and a mean (±SD) of 3.0 (±1.8). The composition of these groups, broken down by group size and type of bee, is given in Fig. 7. In support of P8 and P9, adult males—the greatest contributors to production identified in Fig. 6—are the primary participants in honey collecting groups for the two species of stinging bees. In agreement with P10, parties pursuing the most difficult, dangerous, and skill---intensive giant Asian bee are composed exclusively of adult men (Fig. 6a). Parties pursuing the western---sized bee are composed of a mix of adult men, adolescent males, and women, with a greater frequency of adolescent males and women in larger groups (Fig. 6b). Parties pursuing stingless bees are predominantly composed of adolescent males and women (Fig 6c). These results reflect a progression across bee types as males mature into adulthood, from least to most difficult: stingless bees are targeted by juveniles in order to practice; western---sized bees are targeted by mixed groups that incorporate opportunities for learning; while the most difficult giant Asian bee is only targeted by experienced adult men.

[Fig. 8 about here]

Fig. 8 shows mean total and per capita returns from collecting honey as a function of total group size (panels a and b) and the number of adult men (the most productive sex---age class in identified in Fig. 6; panels c and d). While the largest groups have the highest mean per capita profits, large groups also often return unsuccessfully (7 out of 13 groups pursuing stinging bees with five or more individuals returned without sellable honey). The regressions in Fig. 6 and Table E4 estimate elasticities of production with respect to the total number of group members and number of adult men. Counting all group members, the estimated elasticity of production (1.06, CIs 0.18—1.94) is consistent with constant returns to scale (P11). The elasticity of production counting only adult males is greater (1.51, CIs 0.95—2.07), but with confidence intervals that still include the expectation of constant returns to scale.

[Fig. 9 about here]

Fig. 8 suggests different patterns of returns to scale for the giant Asian versus western---sized bees. In agreement with P12, the highest per capita productivity is observed in larger groups for the giant Asian bee (which benefit from coordinated and complementary roles) but in smaller groups for the western---sized bee (which can be more effectively handled by a small number of people). Fig. 9 shows the mean size of honey collecting parties according to bee type (histograms of party size by bee type are also given in ESM Fig. E5). Consistent with P13, the mean size of parties pursuing giant Asian bees is significantly greater than those pursuing western---sized bees. The mean size pursuing stingless bees falls in an intermediate range between the two stinging bees, with high variance, which may reflect the participation of juveniles and females on the basis of gains to practice and safety in groups, rather than economic efficiency per se.

Discussion

Our two case studies of Tsimane' hunters and Jenu Kuruba honey collectors support the idea that foraging group size and composition are structured according to a division of labor by sex and age and economies of scale in production. They show that the returns to cooperative group formation and individual specialization depend on the character of resources, technologies of acquisition, and other socioecological factors.

In the case of the Tsimane', each of the 13 tested predictions was supported. The results showed that the productivity of additional men (P1) and men's hours (P2) in hunting parties consistently exceeded those of females. These differences in productivity were greater for larger prey and greater skill involved in acquisition (P3). Similarly, the productivity of middle---aged and older men exceeded that of younger males (P4 and P5), with greater differences for larger, more---difficult game species (P6). These differences in productivity were reflected in the composition of hunting parties, which were predominantly composed of men in middle adulthood (P8 and P9). The heterogeneity of group composition was observed to be lower in groups securing larger, more difficult---to---acquire prey (P10).

The Tsimane' results also supported the hypotheses regarding economies of scale. Per capita returns were not lower in parties with more adult male group members (P11), and were higher in large groups for large, cooperatively acquired species such as peccary and tapir (P12). Consistent with higher returns to scale for larger species, groups pursuing these species tended to be larger on average (P13).

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Given the returns to scale for groups of four and five men observed in Figs. 3 and 4, one apparently contradictory finding is that the modal Tsimane' hunting party size was one, with 73% of hunting parties consisting of a solitary hunter. Why was the most commonly observed party size not four? One possible explanation is that on most days, the optimal party size for maximizing per capita returns is close to one. If a hunter leaves his home with no prior knowledge of what he may encounter—including birds, turtles, small mammals, and large mammals—his expected return rate from hunting may be maximized by being alone (or at least an additional hunter might not perceptibly increase expected per capita returns). However, when species that are best hunted in groups are suspected to be present in a given area, cooperative pursuit groups may form with the specific intention of hunting those animals. It may therefore be that the distribution of observed hunting party sizes reflects the distribution of opportunities to achieve economies of scale based on local information. The fact that larger groups capture more large game but less small game *per capita* supports this interpretation. Ethnographically, Tsimane' hunters report and have been observed forming hunting parties explicitly to cooperatively pursue peccaries and tapir.

Other explanations are possible as well. It may be that Tsimane' prefer to hunt solitarily most of the time due to difficulties of coordinating departures with other hunters, risks of free---riding, or other transaction costs [2,10,37]. Hunting independently may also allow sharing partners to reduce variability in the production of meat; given that the Tsimane' mix hunting with horticulture and fishing, sending out hunters on alternate days could help smooth consumption within sharing clusters through time [3,12,20,44]. Distinguishing between these possibilities will require additional research that avoids the problems of self---selection inherent in observational data. A quasi---experimental approach in which incentives were provided to participate in groups of randomly---assigned sizes could examine the differences in per capita returns between experimentally versus naturally formed groups. If hunters are using environmental cues to form groups, naturally formed groups should show higher returns than the experimentally formed groups. Complementarily, 'pre---hunt' interviews could record which species hunters expect to encounter and other information utilized in making decisions, which could then be used to predict the observed size, composition, and productivity of groups.

In the case of Jenu Kuruba honey collectors, we find support for P1, P3, P4, P7---12, and partial support for P13 (P2, P5 and P6 could not be directly tested from the current data). Like the Tsimane', a division of labor by age and sex structures Jenu Kuruba foraging activities. Age and sex are related to the type of honey pursued, the skills used to collect honey, and the returns from collection. The productivity of adult men is greater than that of females or adolescent males, particularly through pursuit of the more dangerous and skill---intensive giant Asian bee (P1, P3 and P4). Adult men are more likely to collect honey from the two species of stinging bees, and are the only age---sex class to collect honey from the giant Asian bee (P7).

We find that honey collecting group composition and economic returns are related to differential productivity in the predicted directions. Females and adolescent males are less likely than adult males to collect honey from the two species of stinging bees, particularly the most difficult and skill---intensive giant Asian bee (P8---10). It is important to note, however, that social norms in the South Indian setting may also prevent females from specializing in honey collecting. While older women have as much explicit honey collection knowledge as men as measured by a verbal exam [36], and girls do participate in 'practice' sessions pursuing stingless bees, females are discouraged from collecting honey as they approach puberty, and women are not allowed to roam in the forest except in large groups or with a male chaperone. The question of whether, all else equal, females could be as proficient at collecting honey as males remains open.

Restrictions on Jenu Kuruba women's movement in the forest raise the more general question of the roles of social norms in either exogenously constraining or serving as a mechanism for realizing efficient divisions of labor between the sexes. Among Hiwi foragers of Venezuela, for example, women are prohibited from touching men's bows and arrows under supernatural threat of infertility [Kim Hill, personal communication]. Among the Aka of central Africa— where there are minimal restrictions on female mobility, easy access to hunting technology, and a pattern of sharing direct childcare responsibilities with men—Noss and Hewlett suggested that local gender norms actually facilitate female participation in net hunting [38]. While there are few explicit restrictions against female hunting among the Tsimane', hunting is normatively recognized as a principally male activity [45].

The productivity of Jenu Kuruba honey collecting groups showed approximately constant returns to scale (P11). Larger groups pursing the giant Asian bee using coordinated cooperative roles (i.e. smoke production and cutting and lowering combs) tended to be achieve higher productivity per capita than smaller groups (P12). P13 was supported by the

observation that groups pursuing the giant Asian bee— which exhibited greater economies of scale—were significantly larger than groups pursuing the western--- sized bee. Groups pursuing stingless bees, however—which show no observable economies of scale in terms of economic production—were generally larger than those pursuing the western---sized bee. This finding reflects the fact that individuals may join groups for different reasons than to maximize direct economic gains. We hypothesize that the larger size of group pursuing stingless may derive principally from the benefits of learning and safety for young honey collectors in larger groups. Uncertain information about the amount of honey in hives, and the difficulty of excluding unwanted "joiners" [10] may also contribute to suboptimal foraging groups, as found in a previous study comparing the Jenu Kuruba with 19th---century Colorado silver prospectors [36].

The two case studies presented in this paper reflect ecologies with rather limited returns to scale. Other ecological conditions would be expected to favor larger groups, or groups with a more structured division of labor and redistribution of returns. Very large game, such as whales, may require a large number of hunters to achieve any success at all [37]. When physical capital investments such as boats or dams are involved in the acquisition of resources, there is likely to be greater scope for larger groups, greater heterogeneity in group membership, and complex divisions of proceeds (e.g. explicit property rights and entitlements). A more general theory of group formation could build on the principles developed in this paper. The division of labor in large---scale complex societies rests in part on these same principles, with even greater degrees of specialization and internal differentiation (e.g. trades and industries), and informal and formal contracts binding relationships in addition to kinship, reciprocity, and other mechanisms that bind together cooperative foraging groups.

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Data accessibility: The data used in this analysis have been anonymized and made available through the Dryad data repository.

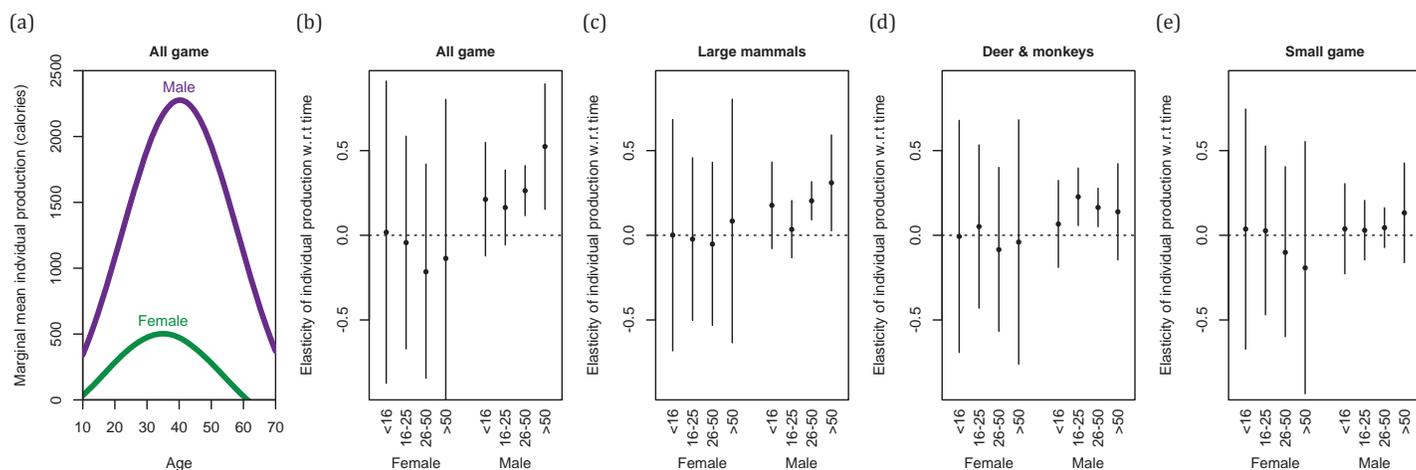## Figures and Figure Captions

Fig. 1. The productivity of individual Tsimane' hunters from encountering and killing prey as a function of age, sex, and time effort (from the regression models in ESM Table E1). (a) Marginal mean production of males and females across life, holding time effort constant. (b) Elasticity of production with respect to time effort for each age-- sex class. (c) Elasticity of production of peccary and other large mammals, excluding deer. (d) Elasticity of production of deer and monkeys. (e) Elasticity of production of small mammals (excluding monkeys), birds, and turtles.

(a) (b)
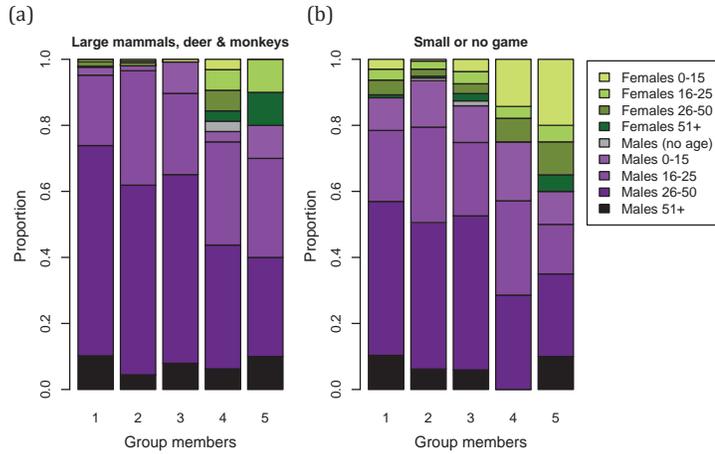
Fig. 2. Age and sex composition of Tsimane' hunting parties as a function of group size and prey type. (a) Parties securing large mammals, peccary, deer, or monkeys. (b) Parties securing small mammals
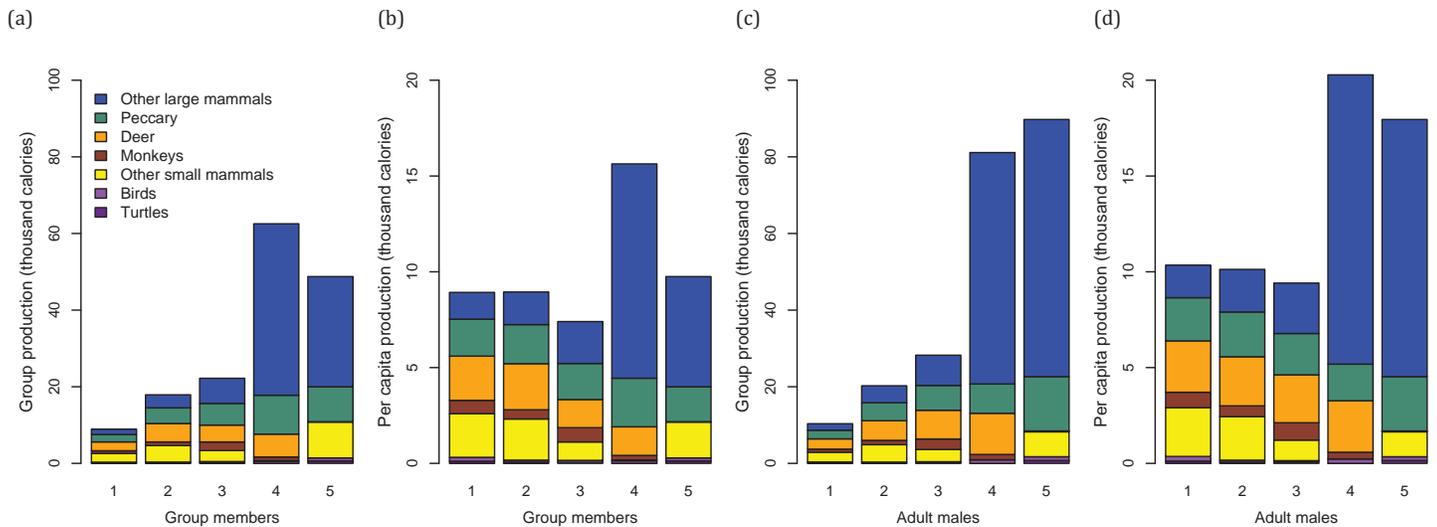(excluding monkeys), birds, or turtles, or failing to secure game.

(a) (b) (c) (d)

Fig. 3. Mean production of Tsimane' hunting parties as a function of group size, stratified by prey type. (a) Total group production by total group size. (b) Per capita production by total group size. (c) Total group production by number of adult males. (d) Per capita production by number of adult males.

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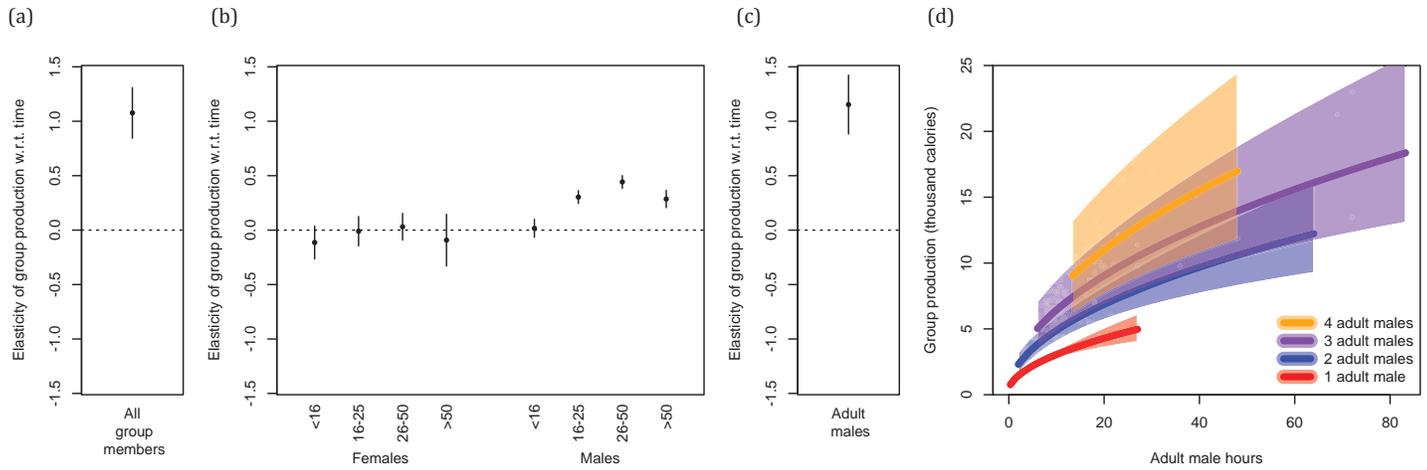
Fig. 4. The productivity of Tsimane' hunting parties as function of the labor inputs of group members (from ESM Table E3). (a) Elasticity of production with respect to the time effort of all group members. (b) Elasticity of production with respect to the time effort of each age-- sex class. (c) Elasticity of production with respect to the time effort of adult males. (d) Estimated total production of hunting groups as a function of the interaction between adult male time effort and number of adult males.
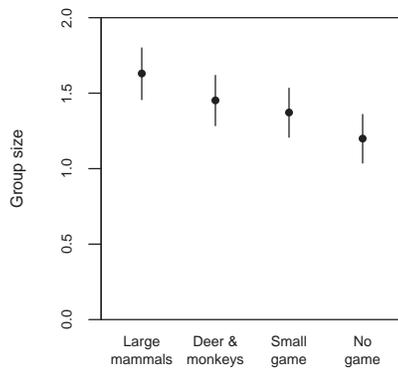

Fig. 5. Mean (±95% CIs) size of Tsimane' hunting parties by prey type. (Categories of game are the same as in Fig. 1.)
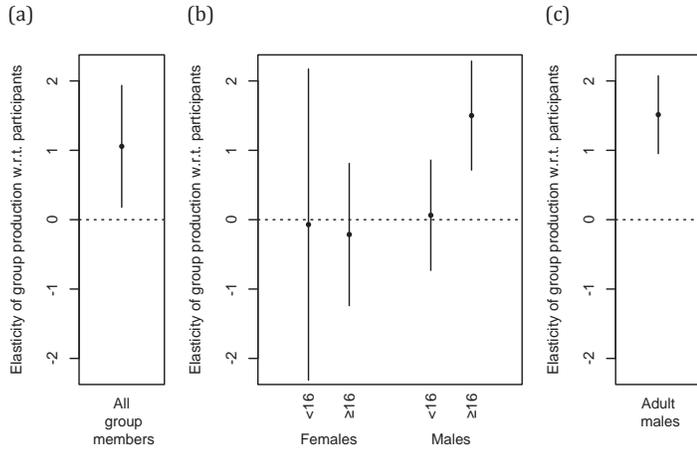
Fig. 6. The productivity of Jenu Kuruba honey collecting parties as a function of the participation of group members (from ESM Table E4). (a) Elasticity of production with respect to total group size. (b) Elasticity of production with respect to the number of group members of each age-- sex class. (c) Elasticity of production with respect to the number of adult males.
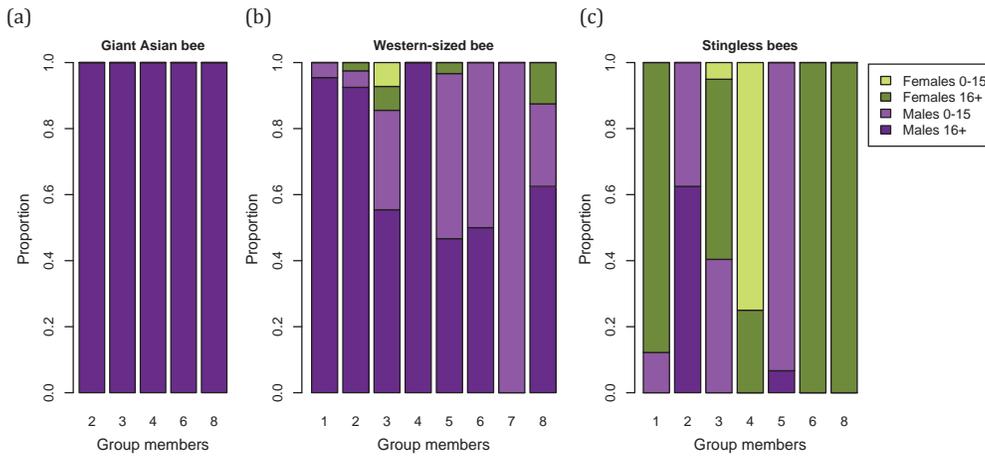

Fig. 7. Age and sex composition of Jenu Kuruba honey collecting parties as a function of group size and bee type. (a) Parties pursuing giant Asian bees. (b) Parties pursuing western-- sized bees. (c) Parties pursuing stingless bees.
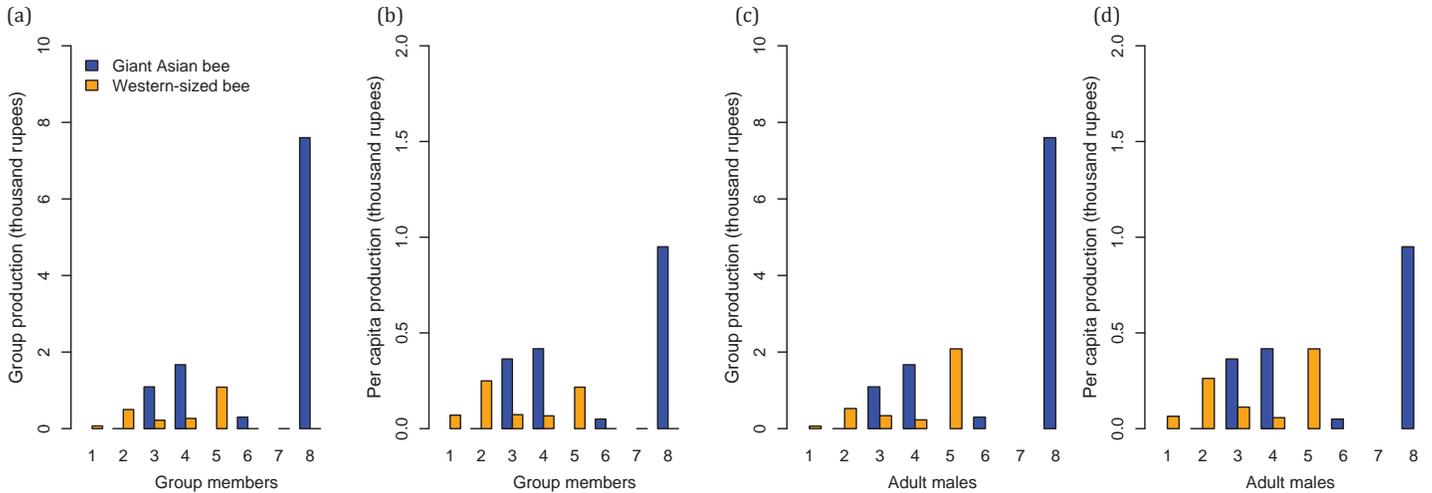
Fig. 8 Mean production of Kuruba honey collecting parties as a function of group size, stratified by bee type. (a) Total group production by total group size. (b) Per capita production by total group size. (c) Total group production by number of adult males.

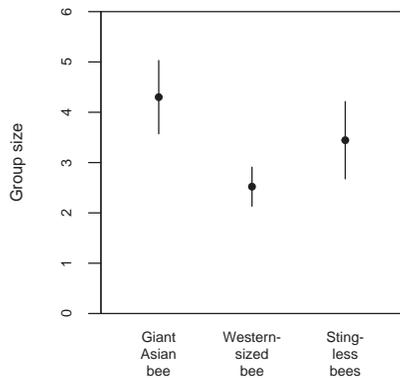(d) Per capita production of number of adult males.

Fig. 9. Mean (±95% CI) size of Jenu Kuruba honey collecting parties for each bee type.

Table

Table 1. Role in Jenu Kuruba honey collecting as a function of age and sex
(multinomial logistic regression with the role of observing as baseline.)

Role (*response*):	Making smoke			Cutting combs			Assisting		
Predictor	*2.5%*	*Est.*	*97.5%*	*2.5%*	*Est.*	*97.5%*	*2.5%*	*Est.*	*97.5%*
Intercept	-9.8	***-9.3**	-8.8	-430.1	-1.6	427.9	-9.4	-1.3	6.8
Female aged <16	-8.9	***-8.9**	-8.9	-24.5	***-24.5**	-24.5	-7.0	1.3	9.6
Female aged ≥16	-1.2	***-1.2**	-1.1	-1268.4	17.1	1302.6	-34.4	-2.4	29.6
Male aged <16	-8.1	***-8.1**	-8.1	-426.1	2.5	431.0	-8.5	-0.3	7.9
Male aged ≥16	8.3	***8.8**	9.3	-425.1	3.4	431.9	-8.0	0.1	8.2
Each observation represent one individual in one honey collecting party; N = 436; *p < 0.05.									