Do Differences In Fruit Abundance Explain Patterns Of Grouping And Intersexual Dominance In Artificial Chimpanzees And Bonobos?

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Table of Contents

Abstract

Although closely related, some female bonobos dominate over males while female chimpanzees do not. The factors influencing the emergence of female dominance over males in bonobos have been heavily debated. Researchers often hypothesize it is because bonobos form larger and more cohesive mixed-sex parties than chimpanzees, supporting the formation of female coalitions against males. Theoretical models also show that the cohesiveness of bonobo parties can lead to female dominance over males through self-organization. Why bonobos form larger mixed-sex parties than chimpanzees remains unclear. Some researchers suggest it is because bonobos experience better ecological conditions than chimpanzees, while others hypothesize it is because female bonobos show prolonged sexual swellings. We investigated whether an increased fruit abundance experienced by bonobos after their divergence from chimpanzees influenced patterns of grouping that supported the emergence of female dominance over males. We created an agent-based model named PanWorld, where virtual entities roamed dynamic environments differing in fruit abundance. Environments with a high abundance of fruit supported the formation of larger parties and females that were more social. However, this did not result in a higher degree of female dominance over males. Due to increased male competition over fruit patches, the degree of female dominance over males was highest in environments with a low abundance of fruit. We argue that such patterns of behavior are not in line with empirical data, and recommend for the addition of behavioral rules that enable PanWorld agents to become better caricatures of bonobos and chimpanzees. All in all, we found that a higher abundance of fruit may explain why bonobos form larger mixed-sex parties than chimpanzees. In nature, increased sociality may lead to female dominance over males. In PanWorld, however, an increase in sociality did not influence the emergence of female dominance over males in line with our hypotheses.

1. Introduction

1.1. Dominance hierarchies

Group living is adaptive because it decreases predation risk and increases access to resources. However, sociality also exacerbates feeding and mate competition (Krause *et al.,* 2002). It is thought that group-living animals minimize intragroup competition and maintain social stability through the establishment of a dominance hierarchy (Hermann, 2017). Dominance hierarchies are social ranking systems often based on agonistic interactions, and the factors underlying their emergence have been heavily debated (Drews, 1993).

The 'prior attributes hypothesis' posits that dominance hierarchies establish from pre-existing differences between individuals, such as their strength, size, or age (Beacham, 1988; Ellis, 1994; Chase *et al.,* 2002). In many species, males are larger than females (Darwin, 1871). Therefore, the prior attributes hypothesis has often been used to explain the prevalence of male-dominated societies. However, sometimes females dominate over males in species where males are larger than females (e.g. White & Wood, 2007). Theoretical models have shown that female dominance over males (from now on called 'female dominance') emerges in societies with sex differences through the winner-loser effect (Hogeweg & Hesper, 1983; Bonabeau *et al.,* 1999; Hemelrijk, 1999; Hemelrijk, 2002; Hemelrijk *et al.,* 2017). The winner-loser effect is a phenomenon where individuals that win fights are more likely to win subsequent fights, and individuals that lose fights are more likely to lose subsequent fights. Empirical evidence for the winner-loser effect has been found in many social animals (Oliveira *et al.,* 2009; Hsu *et al.,* 2009; Franz *et al.,* 2015; Lerena *et al.,* 2021).

1.2. Female dominance in *Pan*

How female dominance emerges in some species remains unclear. This is especially true for chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), where although closely related, female dominance is found in bonobos but not in chimpanzees. Chimpanzees and bonobos are 99.6% genetically identical and share many social and physical characteristics (Prüfer *et al.,* 2012). Both are moderately sexually dimorphic, with males being larger than females, and show sexual swellings associated with estrus (Boesch *et al.,* 2002; Boesch, 2009; Douglas *et al.,* 2016). Both live in fission-fusion societies (Nishida, 1968; Kuroda, 1979), where individuals form subgroups, named parties, that vary temporally in size and composition (Aureli *et al.,* 2008). Despite their similarities, male chimpanzees dominate over all of the females in their group (Foerster *et al.,* 2016), whereas female bonobos have been found to dominate over males or co-dominate alongside males (Kano, 1992; Parish, 1994; Parish, 1996; Furuichi, 1997; Vervaecke *et al.,* 2000).

Many hypotheses have been proposed to explain why some female bonobos dominate over males and chimpanzee females do not. Some researchers claim that female bonobos sexually select for non-aggressive males (Wrangham & Peterson, 1996). Female animals are thought to have leverage over males because they have something males want, fertilizable eggs (Lewis, 2002). Leverage can lead to female dominance because males shouldn't be aggressive towards females if it decreases reproductive success. In support of this, unlike male chimpanzees, male bonobos are not territorial and do not often compete with females (Watts *et al.,* 2001; Boesch, 2009; Hare *et al.,* 2012; Wilson *et al.,* 2014; Gruber & Clay, 2016). However, this hypothesis is weakened by the fact that some male bonobos dominate over females and show aggression toward them (Paoli *et al.,* 2006; Surbeck & Hohmann, 2013). This claim also assumes that males do not sexually coerce females, which is not true for chimpanzees (Muller *et al.,* 2011). As female chimpanzees also have this proposed leverage over males, it remains unclear why female dominance is not found in the species.

Female dominance in bonobos is often associated to their sociality. Compared to chimpanzees, parties in bonobos are larger, more cohesive, and include more females (Furuichi, 2008; 2009; Wakefield, 2008; Wakefield, 2013). Attending larger mixed-sex parties is thought to result in stronger social bonding between female bonobos, which may support the formation of female coalitions (Parish, 1996; Stevens *et al.,* 2006; White & Wood, 2007). Female coalitions control male aggression, causing some female bonobos to dominate over males (Tokuyama & Furuichi, 2016). Theoretical models also show that cohesive groups support the emergence of female dominance through the winner-loser effect. Compared to loose groups,

cohesive groups show a stronger differentiation of the dominance hierarchy, increasing the probability of females becoming dominant over males (Hemelrijk, 2002). Thus, increased sociality, especially that of females, may explain why some females dominate over males in bonobos but not in chimpanzees. However, why bonobos form larger mixed-sex parties than chimpanzees remains not well understood.

1.3. Female sociality in *Pan*

One hypothesis suggests that bonobos form larger mixed-sex parties than chimpanzees because females have prolonged sexual swellings. Both female chimpanzees and bonobos exhibit tumescence, the swelling of visual reproductive organs during ovulation. Tumescence signals fertility and attracts male chimpanzees and bonobos to join parties (Matsumoto-Oda *et al.,* 1998; Hashimoto *et al.,* 2001). In bonobos, tumescence also attracts females and encourages affiliative behaviors among them (Furuichi, 1987, 1989; White, 1988; Wrangham, 2002; Ryu *et al.,* 2015). Bonobos exhibit pseudo-estrus, which are sexual swellings not indicative of ovulation (Douglas *et al.,* 2016). As a consequence, tumescence in bonobos is prolonged and attracts males and females to join parties for extended periods of time. This is thought to result in larger and more cohesive mixed-sex parties in bonobos than in chimpanzees (Furuichi, 2009; Surbeck *et al.,* 2021).

Another hypothesis proposes that bonobos form larger mixed-sex parties than chimpanzees because of decreased food competition. Feeding in parties accelerates the depletion of food patches (Te Boekhorst & Hogeweg, 1994b). As females travel more slowly than males because of their size or the need to carry offspring (Furuichi, 2009), they are often the last to arrive at a food patch. Therefore, it is adaptive for females in scarce environments to be solitary when feeding. Researchers suggest that bonobos experience less seasonality (White, 1998; Yamakoshi, 2004; Murray *et al.,* 2006; Mulavwa e*t al.,* 2008), live in environments with an increased food abundance (Newton-Fisher *et al.,* 2000; Itoh & Nishida, 2007; Pennec *et al.,* 2020), and incorporate more stable fall-back-foods (FBFs) into their diets than chimpanzees (Malenky & Wrangham, 1994; Georgiev *et al.,* 2011; Watts, 2012; Serckx *et al.,* 2015). As a result of decreased food competition, female bonobos are thought to be more social than female chimpanzees, resulting in the formation of larger mixed-sex parties (Hashimoto *et al.,* 2003; Riedel *et al.,* 2011; Lucchesi *et al.,* 2020).

Although both hypotheses have some empirical support, due to a lack of long-term comparative studies, why bonobos form larger mixed-sex parties than chimpanzees remains a major challenge. In this study, we propose another hypothesis to explain why bonobos, especially females, are more social than chimpanzees. Then, we investigate whether this increased sociality explains why some female bonobos dominate over males and female chimpanzees do not.

1.4. The evolutionary history of *Pan*

Researchers often conclude that environmental factors do not significantly vary enough between chimpanzee and bonobo habitats to explain why bonobos form larger mixed-sex parties (Furuichi, 2009). As a result, the hypothesis regarding sexual swellings is often favored over the hypothesis regarding decreased food competition (Surbeck *et al.,* 2021). We agree that chimpanzee and bonobo habitats do not significantly differ today. However, similar to other authors (Hashimoto *et al.,* 2004; Furuichi, 2009), we suggest that the environments bonobos and chimpanzees inhabited in the past did significantly differ. This is because evidence suggests that the divergence of chimpanzees and bonobos from their common ancestor, around 1,290,000 years ago, was influenced by environmental factors (Myers-Thompson, 2003; Caswell *et al.,* 2008). During arid periods of the Pleistocene, many tropical rainforests contracted into fragmented habitats, leading to the diversification of various taxa (Mayr & O'Hara, 1986; Plana, 2004). Researchers found that the divergence of the *Pan* genus occurred because of a major drought along the north of the Congo river (Takemoto *et al.,* 2015). Reduced water levels allowed some individuals to cross from north to south. These individuals became isolated in refugia, environments unaffected by the drought, and evolved into bonobos (Myers-Thompson, 2003; Serckx *et al.,* 2015). The remaining population north of the river evolved into chimpanzees in arid conditions caused by habitat fragmentation (Plana, 2004). This evolutionary history is the basis of our hypothesis.

1.5. Objectives and hypotheses

Empirical evidence suggests that bonobos evolved in environments unaffected by drought, whereas chimpanzees did not (Myers-Thompson, 2003; Takemoto *et al.,* 2015). We aim to investigate whether such conditions, specifically differences in fruit abundance, explain why bonobos form larger mixed-sex parties than chimpanzees. The primary objective of our study is to show that increased fruit abundance increases sociality, especially that of females, without the influence of sexual swellings. We do not introduce tumescence into our model because evidence suggests that prolonged sexual swellings in bonobos evolved after they diverged from chimpanzees (Han *et al.,* 2019). We are interested in social behaviors during the initial stages of *Pan* evolution. Therefore, we want to determine if fruit abundance alone influences grouping patterns that support the emergence of female dominance.

We test whether fruit abundance influences the emergence of female dominance in an agent-based model named PanWorld. Comparative empirical studies on wild chimpanzees and bonobos have proven difficult and may never find the underlying mechanisms behind the emergence of female dominance. This is because it is difficult to disentangle the many influencing variables that are seemingly at play in these species. By using a computational model, we can manipulate variables to investigate how they influence the establishment of a dominance hierarchy.

We hypothesize that, compared to environments with a low abundance of fruit, environments with a high abundance of fruit decrease food competition, supporting the formation of larger mixed-sex parties. As a result, individuals, especially females, are closer to other party members, causing them to engage in more fights. More fights between individuals causes a stronger differentiation of the dominance hierarchy through the winner-loser effect (Hemelrijk, 2002), resulting in a higher degree of female dominance.

2. Methods

2.1. Model description

A general explanation of PanWorld is given here. Detailed explanations of the environment and behavioral rules follow later in the text. PanWorld is an agent-based model created in collaboration with Dr. Hanno Hildenbrandt in C++20. PanWorld is inspired by DomWorld (Hemelrijk, 1999; 2002; Wantia *et al.,* 2003; Hemelrijk *et al.,* 2017), although behavioral rules were adjusted to incorporate the introduction of food and a continuous simulation running time. A timestep in our model is one second. As our model represents a time before the diversification of the *Pan* genus, empirical data of both *Pan* species were used to model agent behavior. In PanWorld, male and female agents (*Pans*) roam a complex dynamic environment containing two types of food, fall-back foods (FBFs) and fruits. Agents follow simple rules of feeding, grouping, and interacting. When individuals are hungry they search for fruit, and if fruits are scarce, some agents search for FBFs. When agents are satiated, they search for other individuals and form parties. If agents come near each other, they can interact, which may be peaceful or agonistic. Agonistic interactions are labeled as 'fights' and represent competition over resources such as food, space, or mating opportunities. As food is included in our model, competition over food patches can lead to fights. However, we do not specify the resources agents compete over, and thus, why individuals enter a fight. Agents have dominance values that reflect their tendency to win a fight. After winning a fight, dominance values are increased and after losing a fight, dominance values are decreased, reflecting the winner-loser effect.

2.1.1. The environment

The environment contains fruits and FBFs. FBFs represent proteinaceous food sources such as pith, terrestrial herbaceous vegetation, and insects (Harrison & Marshall, 2011). FBFs require longer handling times than fruit because they are more fibrous and often require tools to consume (Uwimbabazi *et al.,* 2019). Phenological data were used to determine the abundance of ripe fruit in our environments (Chapman *et al.,* 2005; Uwimbabazi *et al.,* 2019; Pennec *et al.,* 2020; Lucchesi *et al.,* 2020). Specifically, we used data from Chapman *et al.* (2005) on the average proportion of fruiting trees during a drought year (1991), a productive

year (1999), and the highest proportion of fruiting trees in a productive year (1999) in Kibale national park. We assumed that if all trees in a dense rainforest were synchronously fruiting, most of the area would be covered with fruit. As a result, by rounding up the data to the nearest whole numbers, we created environments with 1.0 % (low), 7.0 % (medium), and 13.0 % (high) fruit coverage (Figure 1). These environments represented drought, refugia, and an intermediate of the two.
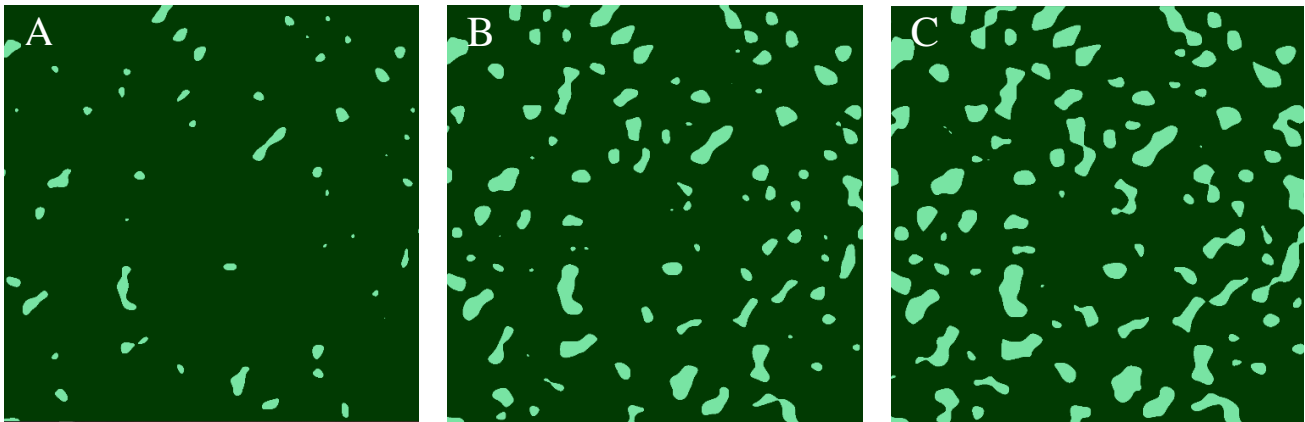

Figure 1. Fruit maps showing the distribution of fruit patches in 0.1 km^2 of environments with a low (A), medium (B), and high (C) abundance of fruit. Fruit patches are light green and open spaces are dark green.

We modelled the distribution of ripe fruit using a Perlin noise function (Perlin, 2002). Perlin noise creates the appearance of realism by generating natural-looking textures. The distribution of trees in rainforests is not completely random (Rozendaal *et al.,* 2020). Perlin noise is characterized by pseudorandom values that do not create any obviously repeating patterns (Perlin, 2002). This added a 'controlled randomness' to our environments, creating natural-looking rainforest patterns, where fruit patches are correlated to each other but appear randomly distributed. Taking inspiration from Te Boekhorst & Hogeweg's (1994a) agent-based chimpanzee model, our environment is dynamic. Although Perlin noise is three dimensional, our environment only contained two dimensions, the *X* and *Y* values. The remaining *Z* value was manipulated to create the illusion of time. How Perlin noise was used to create the environments in PanWorld is explained in Supplementary Figure 1.

Chimpanzees and bonobos use their sense of smell, visual acuity, and spatial memory to find trees containing the highest abundance of ripe fruit (Gilad *et al.,* 2003; Janmaat *et al.,* 2013). While scavenging, they perform goal-directed and cost-effective movements (Jang *et al.,* 2019; Green *et al.*, 2020). They also use Euclidian maps to travel through the core and peripheries of their home ranges (Norman & Boesch, 2009). In PanWorld, agents followed a gradient created by the diffusion of scent coming from fruit patches (Supplementary Fig. 1). Agents followed gradients with the largest magnitudes, representing an individual's ability to find fruit patches containing the most fruit that are nearest to them. Therefore, by following the gradient, agents maximize energy gain and minimize traveling costs.

FBFs are randomly distributed in the environment (Malenky & Stiles, 1991; Morgan *et al.,* 2019). As FBFs represent various 'low-quality' food sources, even drought habitats can be relatively rich in FBFs (Harrison & Marshall, 2011). Therefore, we did not vary the abundance of FBFs between environments. We assumed that only females consumed FBFs because evidence suggests that females require more proteinaceous food than males in both *Pan* species (Uwimbabazi *et al.,* 2021). Also, in both chimpanzees and bonobos, tool use, which is associated with the consumption of insects, is mostly observed in females (Gruber *et al.,* 2010; Sanz & Morgan, 2013).

2.1.2. Behavioural rules

2.2.2.1. *Pan* agents

Agents have a position in the environment (**r**) and an energy value (E) (Table 1). Agents have the goal of consuming 2000 calories a day and lose calories at the rate E_{loss} (Table 2). Agents do not sleep, meaning that a day is defined as 12 hours. Individuals are hungry when their energy value drops below E_{hungry} and are satiated when it reaches E_{full} (Table 2). Agents consider others to have entered their personal space when they are within *PerSpace* of each other (Table 1). Females prioritize FBFs when they perceive the magnitude of the gradient to be smaller than A_{low}. Correspondingly, while searching for FBFs, if females perceive the magnitude of the gradient to be larger than A_{high}, they prioritize the search for fruit (Table 1). Females find FBFs with a probability of P_{FBF} (Table 1). Bonobos and chimpanzees have home-ranges that they have a good memory of and can communicate with party members over long distances (Norman & Boesch, 2009). Therefore, we assume that agents form parties topologically. This means that individual find and group with a fixed number of their nearest neighbors (*TopologicalRange*) irrespective of distance (Table 1).

Agents have a dominance value (*Dom*) and an aggression factor that scales the impact of fights (*StepDom*) (Table 1). A high *StepDom* represents a violent fight and leads to a large change in an individual's dominance value. Comparatively, a low *StepDom* reflects a mild agonistic interaction, meaning that the outcome of a fight impacts an individual's dominance value to a lesser extent. Both *Pan* species show a moderate degree of male-biased sexual dimorphism. To reflect this, females in PanWorld had a slightly lower *StepDom* than males, representing their lower intensity of aggression. For the same reason, males were initiated with higher *Dom* values than females.

Table 1. PanWorld agent parameters. Sex indicated by F (female) and M (male).

Parameter		Description	Value at initialization	References
Dynamic	**r**	Position in the environment	Within *PartySpace* of *PartySize* individuals where parties have a density of *PopDensity* (Table 4)	Furuichi (2009)
	E	Energy value	(5.00 - 15.00 kcal)	*Model assumption*
	Dom	Dominance value	8.0 (F), 16.0 (M)	Hemelrijk (1999); (2002); Wantia *et al,* (2003); Hemelrijk *et al.* (2017)
Static	*PerSpace*	Personal space radius	2.0 m	Hemelrijk (1999); (2002); Wantia *et al,* (2003); Hemelrijk *et al.* (2017)
	StepDom	Aggression factor that scales the outcome of fights	0.8 (F), 1.0 (M)	Hemelrijk (1999); (2002); Wantia *et al,* (2003); Hemelrijk *et al.* (2017)
	A_{low}	Gradient threshold for prioritizing FBFs	0.05 (F), 0.0 (M)	*Model assumption*
	A_{high}	Gradient threshold for prioritizing fruit	0.1 (F), 0.0 (M)	
	TopologicalRange	Number of closest nearest neighbors agents want form a party with	10	Furuichi (2009)
	P_{FBF}	Probability of finding a FBF patch per timestep	0.0005	*Model assumption*

Table 2. PanWorld parameters influencing the energy value of an agent.

Parameter	Description	Value	References
E_{loss}	Rate of energy loss per timestep	(0.04 - 0.06) kcal/s	Uwimbabazi *et al.* (2019)
E_{fruit}	Rate of energy gain from eating fruit	0.2 kcal/s	
E_{FBF}	Rate of energy gain from eating FBFs	0.1 kcal/s	
E_{max}	Maximum possible energy value	250.0 kcal	Chemurot *et al.* (2012)
E_{min}	Minimum possible energy value	0.0 kcal	*Model assumption*
E_{hungry}	Energy level when an individual is considered hungry	(0.0 – 20.0) kcal	Chemurot *et al.* (2012)
E_{full}	Energy level when an individual is considered satiated	(230.0 – 250.0) kcal	

Agents perform many actions. They follow the gradient of fruit scent to find or move away from fruit patches. To find other individuals and form parties, agents follow the direction of the average location of a number (*TopologicalRange*) of their closest nearest neighbors. Agents also perform random wanders (*Wiggle*), avoid others by keeping them a certain distance away from them (*Avoidance*), align their heading with their party members (*Align*), and interact with each other. These actions require changes in position, which we will now discuss.

2.2.1.2. *Pan* movement

Agents perceive a lot of information about the environment and themselves, such as their energy value, the location of their closest nearest neighbours, and the direction towards fruit patches bearing the most fruit. Individuals prioritize what information to use depending on their current state. Agents change their position by following a certain direction with a certain speed. An individual's position in the next timestep is given as follows:

$$r_i = r_i + (S_{state} \times d_i) + r_{avoid_i} \tag{1}$$

Where S is their speed and d_i (direction) is calculated using the vector v_i:

$$v_i = (w_{prev} \cdot d_{prev}) + (w_{food} \cdot d_{food}) + (w_{group} \cdot d_{group}) + (w_{align} \cdot d_{align}) + (w_{wiggle} \cdot d_{wiggle}) \tag{2}$$

This is normalized to give their heading:

$$d_i = \frac{v_i}{|v_i|} \tag{3}$$

The heading is the sum of multiple direction vectors (Eq. 2 & Table 3). These direction vectors have accompanying weighting factors (*w*) associated with them. How different direction vectors are weighted define the movement of agents in different states (Supplementary Table 2).

Table 3. Direction vectors available to a PanWorld agent.

Direction vectors	Description
d_{prev}	Direction towards your previous heading
d_{food}	Direction towards fruit patches
d_{group}	Direction towards the centre of *TopologicalRange* individuals
d_{align}	Direction of the average heading of your current party
d_{wiggle}	Direction that results in a random wander

Another aspect of agent movement is called *Avoidance*, which is made up of w_{avoid} and *dist$_{avoid}$*. *Avoidance* determines how close individuals want to be to each other. *dist$_{avoid}$* establishes the distance between individuals, while w_{avoid} is a weighting factor that influences how strongly agents follow this rule. Therefore, a larger w_{avoid} ensures that individuals adhere very strictly to keeping *dist$_{avoid}$* distance away from each other. A smaller w_{avoid} can cause individuals to be within *dist$_{avoid}$* of each other. *Avoidance* is implemented in our model as the displacement of an agent (Eq. 2). Avoidance is represented by the vector $\boldsymbol{r}_{avoid_i}$, which is calculated as follows:

$$\boldsymbol{r}_{avoid_i} = \sum_{j=1}^{TopologicalRange} (w_{avoid_{state}} \times (dist_{avoid_{state}} - dist_{ij}) \times \boldsymbol{d}_{ij} \qquad (4)$$

where *dist$_{ij}$* is the distance and $\boldsymbol{d}_{ij}$ the direction towards an individual within *TopoligicalRange. Avoidance* parameters are state-dependant (Supplementary Table 2).

2.2.1.3. *Pan* states

Agents in our model occupy states within the PanWorld state-machine (Fig. 2). We will go through this state-machine, explaining what actions agents perform and why agents enter and leave each of the states.

Engage

Every second, an agent checks whether there is an available *InteractionPartner*. An available *InteractionPartner* is defined as an individual within *PerSpace* that is currently not interacting with anyone else. If this is not the case, the agent will remain in its current state. If there is an available *InteractionPartner*, a mental battle is performed. A mental battle is a prediction made by agents on the probability to win a fight against another individual. The mental battle is performed using the *DomRatio*:

$$DomRatio_{ij} = \left(\frac{Dom_i}{Dom_i + Dom_j}\right) \qquad (5)$$

where *Dom$_i$* is the initiating individual's dominance value and *Dom$_j$* is the dominance value of the available *InteractionPartner*. The *DomRatio* is used as a probability to draw from a Bernoulli distribution to either predict a win (1 is drawn) or a loss (0 is drawn). If a win is predicted, both individuals enter the Interacting state. If a loss is predicted, the initiating individual ignores the other and remains in its current state. After losing a mental battle, agents ignore all other available *InteractionPartners* for 20 seconds. This is done to minimize reoccurring mental battles against the same agents. However, during this time, agents can still enter an interaction passively due to another individual winning a mental battle against them. If there are multiple *InteractionPartners* within *PerSpace,* the closest agent is chosen for the mental battle.

SearchingFruit

Agents enter the SearchingFruit state when they are hungry ($E_i \leq E_{hungry}$). During this state, they follow the fruit scent gradient with the largest magnitudes towards fruit patches. When agents are in SearchingFruit, they move slightly away from their group to minimize food competition. Once a fruit patch is found, they enter the EatingFruit state. If females perceive little fruit around them (magnitude of noise gradient ($Grad_{mag}$) $< A_{low}$), they enter the SearchingFBF state.

SearchingFBF

Females in SearchingFBF stay away from their group to minimize food competition and perform a random wander until they find FBFs. When they do so, they enter the EatingFBF state. If females in SearchingFBF perceive a fruit patch to be nearby (magnitude of noise gradient ($Grad_{mag}$) $> A_{high}$), they prioritize fruit and enter the SearchingFruit state.

EatingFruit

Agents enter the EatingFruit state when they enter a fruit patch. While eating, individuals move very slowly. Patches can change while individuals are on it due to the dynamic environment. Therefore, agents can 'fall off' patches while eating. When this happens, agents enter the SearchingFruit state to re-find the patch. While in the EatingFruit state, an individual's energy is updated as follows:

$$E_i = E_i + E_{fruit} \qquad (6)$$

Individuals eat until they are satiated, which occurs when:

$$E_i \geq E_{full}$$

When satiated, individuals enter the Resting state. After feeding, E_{full} and E_{hungry} are re-drawn from the same distribution of which they were initialized from (Table 2). This introduces stochasticity to the timing of state changes, meaning that individuals do not become hungry or satiated at the exact same time.

EatingFBF

The same rules apply for the EatingFBF state as they do for the EatingFruit state. The only difference is that individuals eat FBFs and their energy is updated as follows:

$$E_i = E_i + E_{FBF} \qquad (7)$$

Resting

Individuals enter the *Resting* state when they are satiated. Unless interrupted by an interaction, individuals rest for 300 seconds. During this time, individuals stay close to the food patch they just ate from. After resting, individuals enter the Grouping state.

Grouping

Agents enter the Grouping state when they are satiated and have rested. Here, individuals try to find others by moving in the average direction of *TopologicalRange* individuals. If agents find each other, they move together as a party. This means that the headings of the individuals within the party are aligned. Agents in parties mostly keep to open spaces but can move through food patches and come in contact with individuals who are searching for food, eating, or resting. While grouping, individuals try to keep some distance between themselves and their party members. This is because there is no reason to compete over food when you are not hungry. However, they can come near (within *PerSpace*) to their party members by accident. Agents leave the Grouping state and enter the SearchingFruit state when they are hungry, which is when:

$$E_i \leq E_{hungry}$$

Interacting

Agents enter the Interacting state if they won a mental battle against an available *InteractionPartner* or if someone won a mental battle against them. During this state, they stay close to their *InteractionPartner*. Based on observations of Goodall (1968), the Interaction state lasts 5 seconds. During an interaction, both agents calculate the *DomRatio_{ij}* with themselves as *i* (Eq. 5). These are used as a probability to draw from a Bernoulli distribution to assess the outcome of the interaction (*W*), which is either a 0 (loss) or a 1 (win). Therefore, there are four possible interaction outcomes:

1. *Lose-Lose*
   - Both individuals draw a 0 and choose not to fight. In this case, both individuals leave the Interacting state and enter the PeacefulInteraction state. Due to the manner of how interaction outcomes are determined, this outcome will occur most often between individuals of a similar rank. *Dom* values are not updated after a *Lose-Lose* outcome.

2. *Lose-Win*
   ▪ The initiating individual draws a 0 (W_i) and their opponent draws a 1 (W_j). This results in a fight between the two individuals with the opponent winning against the initiating individual. Their *Dom* values are updated as follows:

$$Dom_i = Dom_i + \left(\left(W_i - DomRatio_{ij}\right) \times StepDom_i\right)$$
$$Dom_j = Dom_j + \left(\left(W_j - DomRatio_{ij}\right) \times StepDom_i\right)$$

(8)

   Equation 8 reinforces that a victory that is expected (high-ranking individual winning against a low-ranking one) changes the *Dom* values of both opponents to small degree, whereas an unexpected victory has more impact on the dominance ranks of the individuals. After the fight, the winner, which is the opponent (*j*), leaves the Interaction state and enters the RefractoryPeriod state. The loser (*i*) enters the Fleeing state.

3. *Win-Lose*
   ▪ The initiating individual draws a 1 (W_i) and the opponent draws a 0 (W_j). This results in a fight between the two individuals with the initiating individual winning against the opponent. Their *Dom* values are updated (Eq. 8). The winner of the fight, which is the initiating individual (*i*), leaves the Interacting state and enters the RefractoryPeriod state. The loser (*j*) enters the Fleeing state.

4. *Win-Win*
   ▪ Both individuals draw a 1, meaning there is no clear winner or loser. Both individuals perform the fight again until there is clear winner or loser or until both decide to have a peaceful interaction. Therefore, both individuals re-enter the Interaction state and *Dom* values are not updated until there is a clear outcome of the fight. Emergently, this fight takes a longer amount of time and is thus considered as 'intense'. Similarly to *Lose-Lose*, this interaction outcome will occur most often between individuals of a similar rank.

Dom values cannot go lower than a value of 0.0001 or higher than a value of 100.0.

Fleeing

Agents enter the Fleeing state after losing a fight. During this state, individuals flee from the winner and the fruit patch they possibly fought over. After fleeing for 20 seconds, agents return to the state they were in prior to the interaction.

PeacefulInteraction

Individuals enter the PeacefulInteraction state if both agents draw a 0 during an interaction. This state lasts for 20 seconds, during which both *InteractionPartners* stay close together. After a peaceful interaction, agents enter the RefractoryPeriod state.

RefractoryPeriod

Agents enter the RefractoryPeriod state after winning a fight or after a peaceful interaction. This state lasts for 20 seconds. After the refractory period, agents enter the state they were in prior to the interaction. This state is crucial for controlling the frequency of individuals re-entering interactions with the same agents.
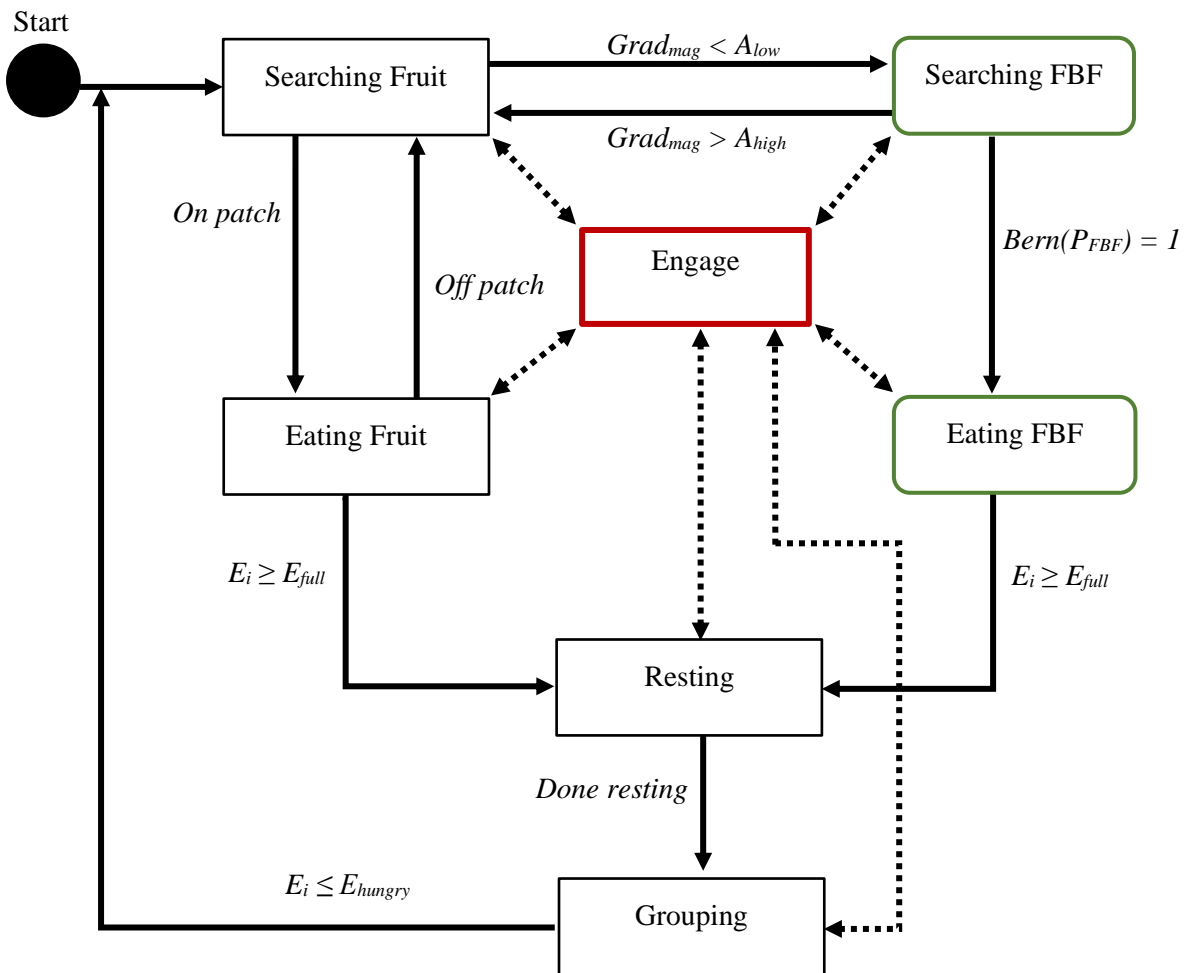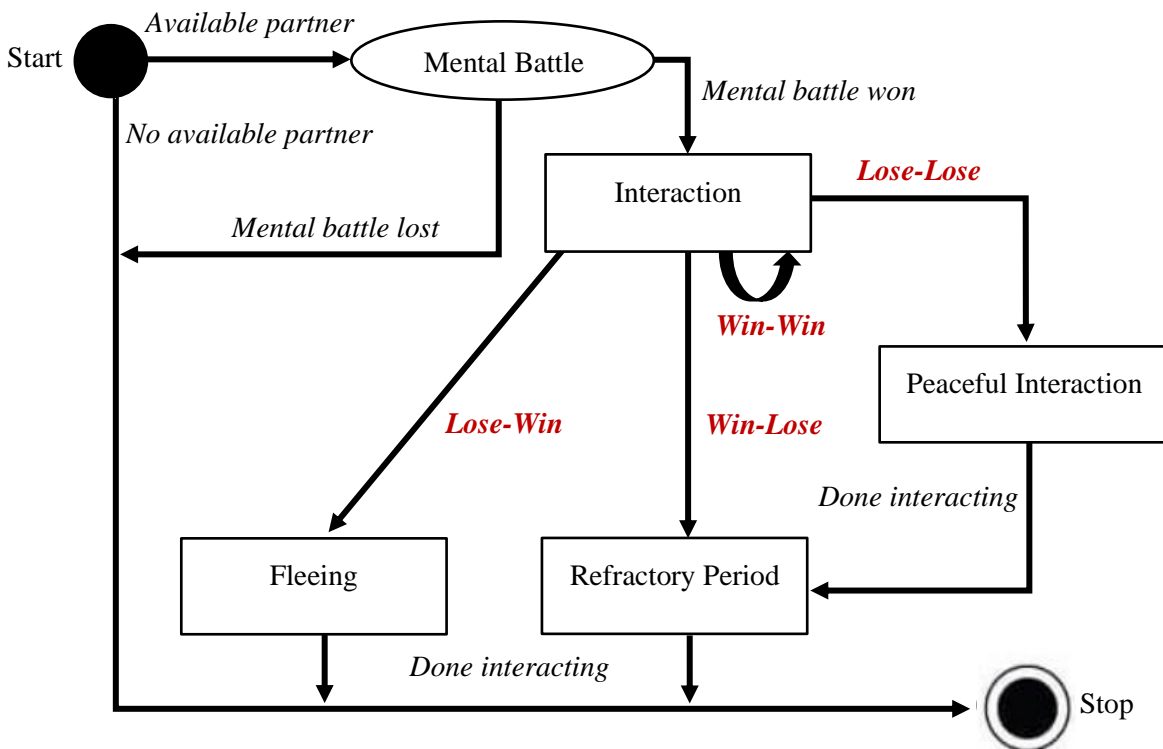
Figure 2. PanWorld state diagram showing why agents change from one state to the other. Green outlines are associated with exclusive female states and red bold lettering are interaction outcomes. Dotted lines are associated with going in and out of engage. State changes are fully explained in the text.

2.2.1.3. Agent initialization

In tables shown above (Table 1 & Table 2), parameters such as E_{loss} have ranges given for their initialization. This means that the initial values were drawn from a normal distribution in the given ranges. This variation is created to represent differences in metabolisms and allow for stochasticity in the timings of state changes. Parameters without ranges were initialized with the values given in the tables. The environment was inhabited by N_{fem} number of females and N_{male} number of males (Table 4). Individuals were initialized in parties of *PartySize*, where each agent was at least *PartyRadius* away from another individual (Table 4). These initial parties were distributed in the environment with a density of *PopDensity* (Table 4).

Table 4. PanWorld party initialization parameters.

Parameter	Description	Value
N_{fem}	Number of female agents	25
N_{male}	Number of male agents	25
PopDensity	Initial density of parties	$1/km^2$
PartyRadius	Party defining radius	30 m*
PartySize	Initial party sizes	10 agents

*inspired by Van Leeuwen *et al.* (2020)

2.2. Data collection and statistical analyses
20 replicate simulations of the environments with a low, medium, and high abundance of fruit were run for 2 weeks. During the simulations, we continuously measured the calories consumed, distance traveled, and the time spent solitary, grouping, and feeding for all agents. We also measured party sizes every hour. We kept track of whom agents were interacting with and the type of interactions that were occurring. Dominance values and outcomes of fights were continuously kept track of.

Data analysis was done in R (version 4.2.1). Figures were created using the GGPlot2 package (version 3.3.6) and statistical analyses were done using the RStatix package (version 0.7.0). We used the Shapiro-Wilks test to determine whether data were normally distributed. Statistical tests regarding multiple comparisons between the three environments were done using a one-way ANOVA with a Tukey's HSD post-hoc pairwise comparison (normally distributed data) or a Kruskal-Wallis test using a Dunn's test (Bonferroni correction) as a post-hoc pairwise comparison (non-parametric data). For comparisons made between the sexes, a Wilcoxon signed-ranks test was used. When making comparisons between environments, we utilized data from the last day of each of the replicates. This allowed us to look at patterns of behavior when the dominance hierarchy had been established and stabilized. For measurements that required data across multiple days, such as the number of fights won, we introduced a 'burn-in'. We omitted the data from the first day, which ensured that we did not introduce any initialization biases into our measurements.

To measure the steepness of the dominance hierarchy, we calculated the coefficient of variation of *Dom* values at the end of the simulation. The coefficient of variation is the standard deviation of the *Dom* values divided by the mean. The dominance hierarchy was created by ranking individuals according to the average dominance index (ADI). The higher the ADI, the higher an individual's dominance position. The ADI for an agent was calculated as the ratio of the number of conflicts won over another individual, divided by the total number of conflicts with that agent. We calculated the mean ADI for each individual, excluding dyads that did not interact from the calculation. We calculated the degree of female dominance in the population as the relative position of females over males in the dominance hierarchy. This is called the female dominance index (FDI) and was measured using the standardized Mann-Whitney U value (Hemelrijk *et al.*, 2008).

Within the dominance hierarchy, we counted the number of females ranking above each male, then the value of the statistic is computed as the sum of these counts, divided by the maximum possible value for the sex ratio and size of the population (Hemelrijk *et al.*, 2008).

3. Results

We ran simulations of our model PanWorld and investigated whether the abundance of fruit influenced grouping patterns that supported the emergence of female dominance in virtual *Pans*. We will first look at how fruit abundance affected the composition of the female diet. Then, we will look at differences in grouping patterns between environments and how this influenced the occurrence of different dyadic interactions and the emergence of female dominance.

3.1. Female diet and distance traveled

A decrease in fruit abundance caused females to consume a significantly higher proportion of FBFs but did not significantly affect their overall calorific consumption (Fig. 3 & Supplementary Table 3). As FBFs take longer to consume than fruits, females spent more time feeding than males in all of the environments (Supplementary Fig. 3B). Due to competition over fruit patches, males traveled significantly more kilometers a day than females in each of the environments (Supplementary Fig. 2). As female fruit consumption increased, so did their daily travel distance (Supplementary Fig. 2). Comparatively, an increase in fruit abundance decreased daily travel distance in males due to a decrease in competition (Supplementary Fig. 2).
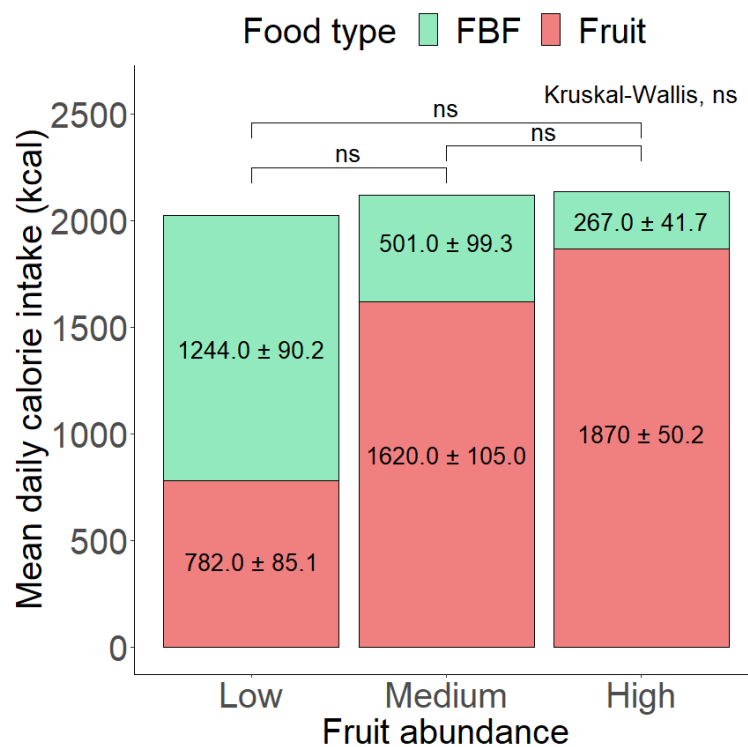

Figure 3. The mean daily calorie intake of PanWorld females in environments differing in fruit abundance. Fruit intake is shown in red (bottom part of stack) and fall-back food (FBF) intake is shown in green (top part of stack). Variation among replicate simulations ($N = 20$) is indicated by standard deviation. Statistical results in the figure test for differences in overall calorie consumption. ns = $P > 0.05$.

3.2. Grouping

Male and female solitariness significantly increased with a decrease in fruit abundance (Fig. 4 & Supplementary Tables 3 & 4). As females spent more time feeding and less time grouping (Supplementary Fig. 3), they were significantly more solitary than males in all of the environments (Fig. 4 & Supplementary

Table 5). Larger parties formed in environments with higher fruit abundance (Fig. 5). In environments with a low abundance of fruit, agents were mostly found as pairs and the average party size was 4.32 (Fig. 5). In environments with a medium and high abundance of fruit, agents were mostly found in parties of six and the average party size was 5.45 (medium) and 5.47 (high) (Fig. 5). Thus, an increase in fruit abundance decreased solitariness, especially in females, causing the formation of larger parties.
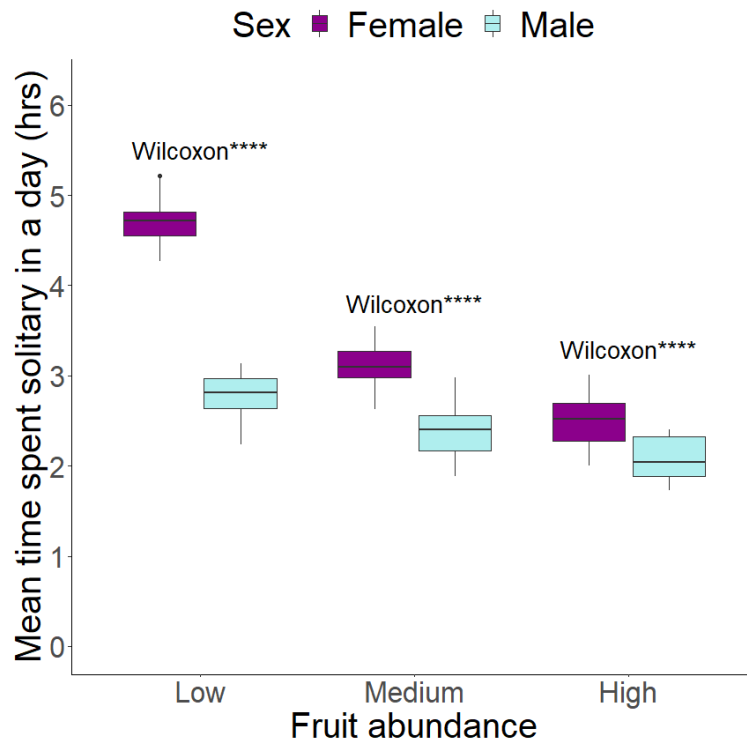

Figure 4. The mean time spent solitary in day for PanWorld females (purple) and males (blue) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). **** = $P \leq 0.0001$.
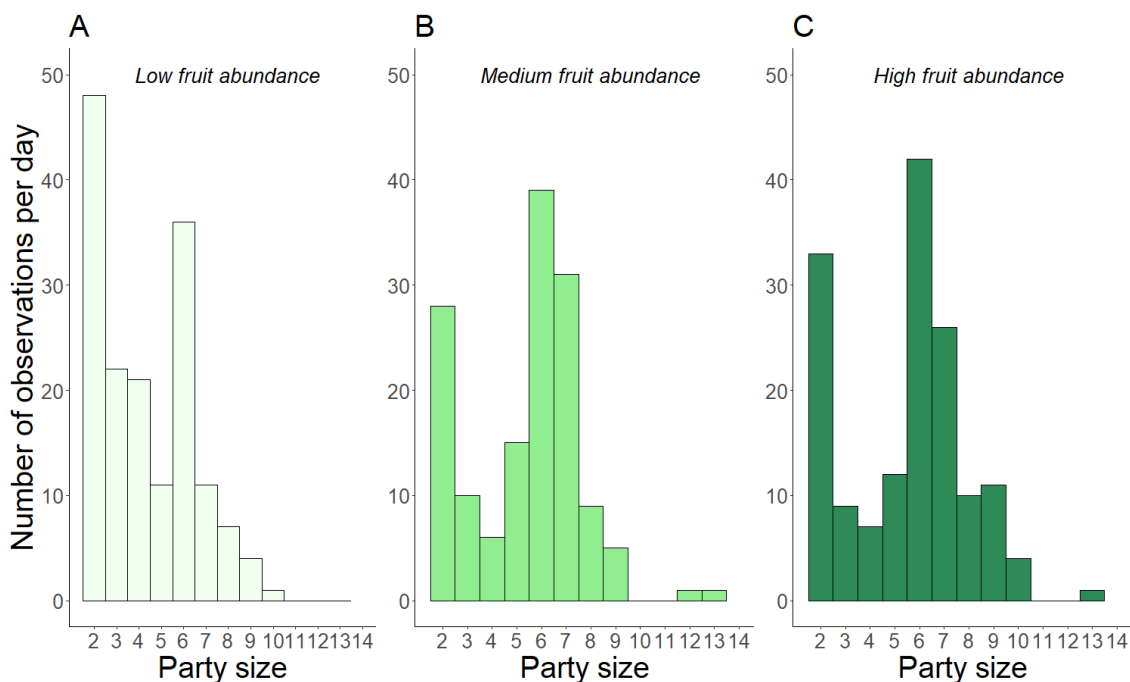

Figure 5. The daily number of observations of varying party sizes observed in environments with a low (A), medium (B), and high (C) abundance of fruit. Data taken from 20 replicate simulations of each environment.

16

3.3. Interactions

Surprisingly, although individuals were more solitary, a decrease in fruit abundance significantly increased the daily number of interactions males and females were involved in (Fig. 6 & Supplementary Tables 3 & 4). This is because a decrease in fruit abundance led to an increase in competition over fruit patches. As females prioritized FBFs when fruits were scarce, they entered fewer competitions over fruit patches than males. Thus, males significantly interacted more than females, especially in environments with a low abundance of fruit (Fig. 6 & Supplementary Table 5).
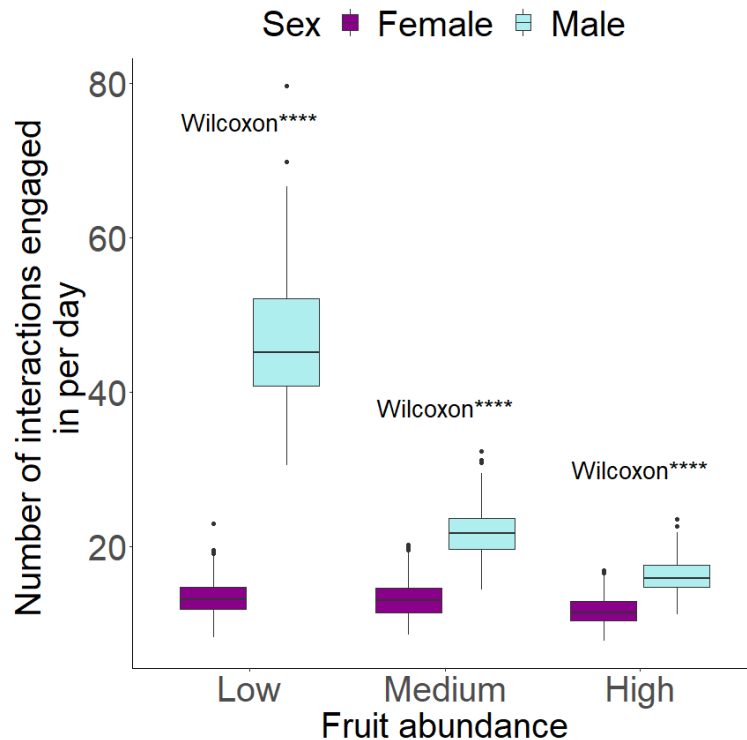

Figure 6. The daily number of interactions engaged in for PanWorld females (purple) and males (blue) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). **** = $P \leq 0.0001$.

An increase in fruit abundance significantly increased the proportion of female-female fights, decreased the proportion of female-male fights, increased the proportion of male-female fights, and decreased the proportion of male-male fights (Fig. 7 & Supplementary Table 6). Due to increased competition over fruit patches, most agonistic interactions in environments with a low abundance of fruit occurred between males (Fig. 7). Contrastingly, with more female attendance in parties, agonistic interactions in environments with a medium and high abundance of fruit mostly occurred between males and females (male initiated). The least occurring agonistic interactions in environments with a medium and high abundance of fruit were between females and males (female initiated) (Fig. 7). In environments with a low abundance of fruit, between female fights were the least occurring agonistic interaction because of the increased solitariness of females.

The proportion of peaceful interactions significantly increased with an increase in fruit abundance for both sexes (Fig. 8 & Supplementary Table 7). The highest proportion of peaceful interactions was found in environments with a medium abundance of fruit, and peaceful interactions mostly occurred between intrasexual dyads (Fig. 8 & Supplementary Table 7). Males had a larger proportion of peaceful interactions than females in all cases except for intersexual dyads in environments with a low abundance of fruit (Fig. 8 & Supplementary Table 7).
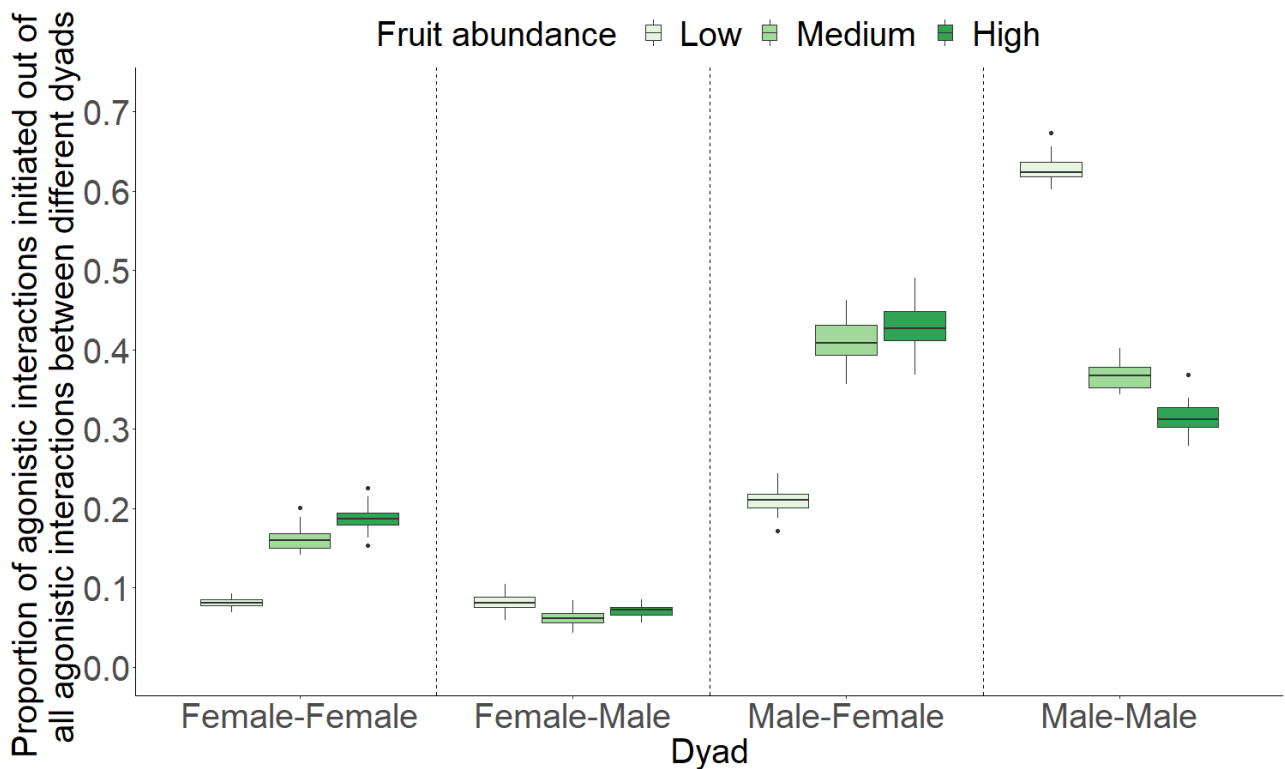
Figure 7. The proportion of agonistic interactions initiated between different PanWorld dyads in environments with low (light green), medium (green), and high (dark green) abundance of fruit. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$).

Figure 8. The proportion of intrasexual (light purple) and intersexual (dark purple) peaceful interactions initiated by PanWorld females (A) and males (B) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$).
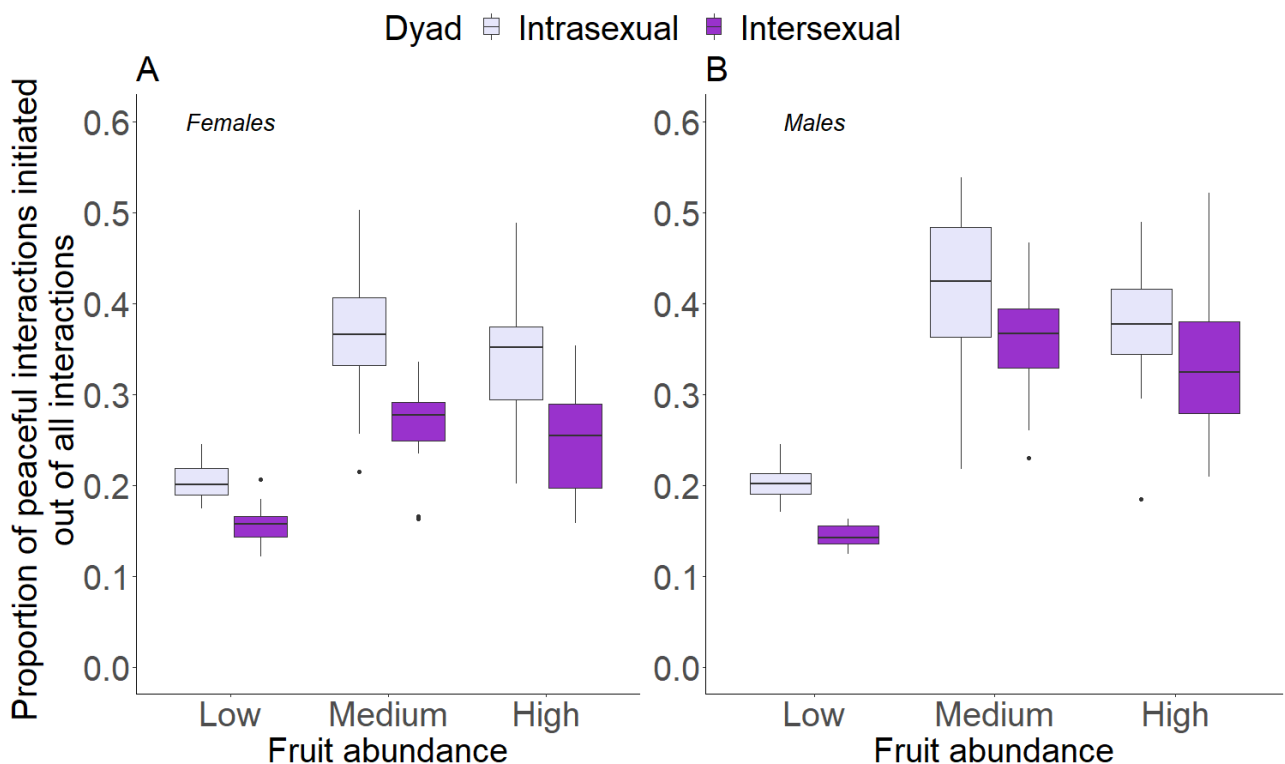
3.4. Female dominance

Environments with a medium and high abundance of fruit supported the emergence of females with very high *Dom* values (close to highest of the total population) to a greater extent than environments with a low abundance of fruit (Supplementary Fig. 6). However, this did not result in a higher degree of female dominance as FDI significantly decreased with increased fruit abundance (Fig. 9 & Supplementary Table 8).
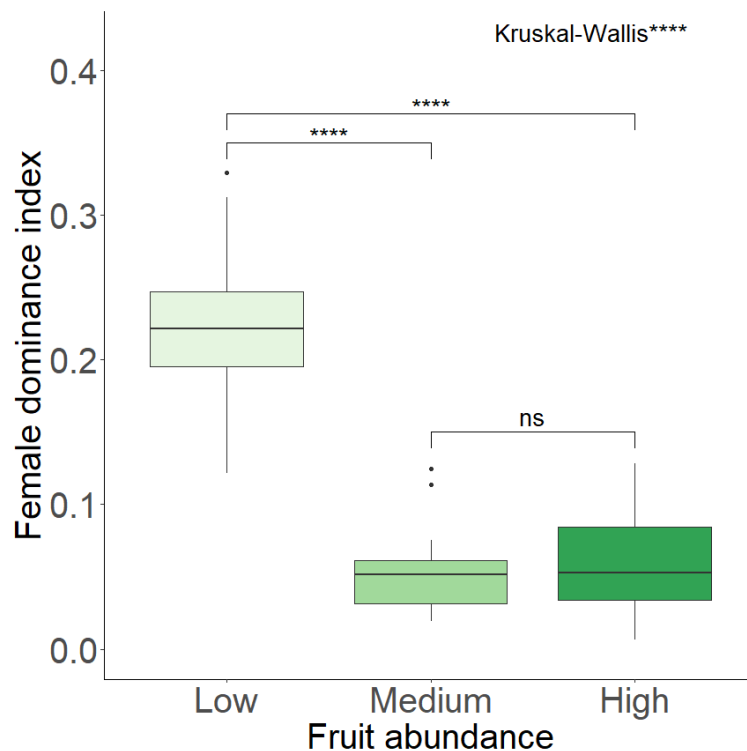

Figure 9. The degree of female dominance (calculated using the female dominance index) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). ns = $P > 0.05$ and **** = $P \leq 0.0001$.

A decrease in fruit abundance resulted in a higher FDI because male *Dom* values in such environments were more strongly differentiated. This was due to an increase in agonistic interactions over fruit patches, which increased the steepness of the dominance hierarchy (Fig. 10A & Supplementary Table 8), causing some females to rank above males (Supplementary Fig. 7A). With some males ranking below females, females in environments with a low abundance of fruit initiated more interactions with males than in other environments (Supplementary Fig. 4). This also led to an increase in the proportion of female-male agonistic interactions (Fig. 7). Contrastingly, when females and males were closer in rank in environments with a medium and high abundance of fruit, females had more intersexual win-win fight outcomes (Supplementary Fig. 5A).

The steepness of the male dominance hierarchy significantly decreased with an increase in fruit abundance (Fig. 10C & Supplementary Table 8). Consequently, the mean final *Dom* values of males in environments with a high abundance of fruit were significantly lower than those in environments with a medium abundance of fruit (Supplementary Fig. 8B). Interestingly, the female dominance hierarchy significantly increased in steepness from environments with a low to medium abundance of fruit, but then significantly decreased environments with a medium to high abundance of fruit (Fig. 10B & Supplementary Table 8). Female and male dominance hierarchies had a similar steepness in environments with a low abundance of fruit but, due to females entering more fights against males, and males entering less fights against other males, an increase in fruit abundance caused females to have a steeper dominance hierarchy than males (Fig. 10).
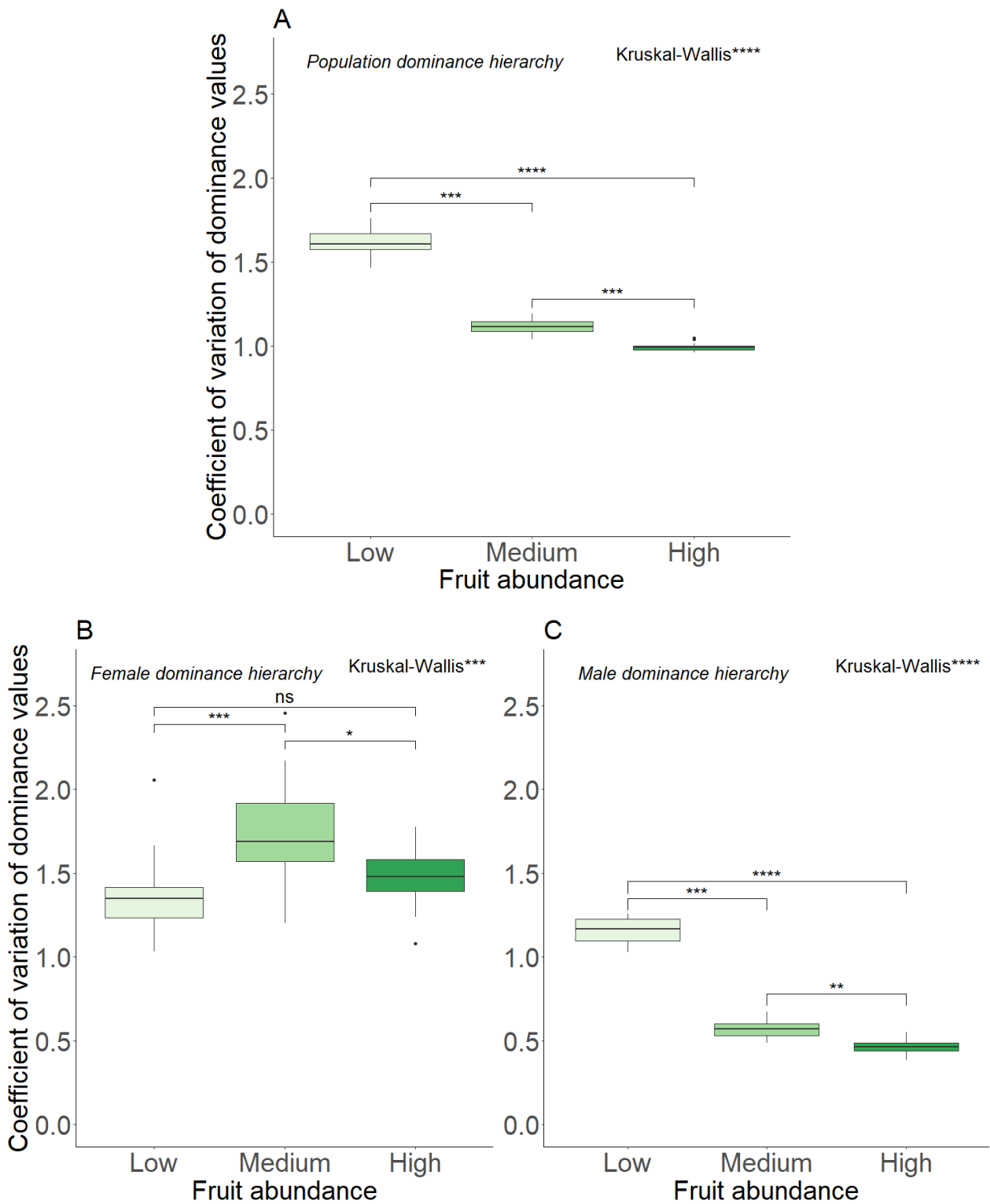
Figure 10. The coefficient of variation of dominance values (steepness of the dominance hierarchy) of the entire PanWorld population (A), only females (B), and only males (C) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). ns = $P > 0.05$, * = $P \leq 0.05$, ** = $P \leq 0.01$ *** = $P \leq 0.001$, and **** = $P \leq 0.0001$.

4. Discussion

4.1. Sociality

Results from the model PanWorld support the first part of our hypothesis that proposed that an increase in fruit abundance increases sociality. Larger parties formed in environments with a higher abundance of fruit because individuals, especially females, were less solitary. An increase in fruit abundance decreased female solitariness because it caused them to consume fewer FBFs. FBFs are proteinaceous food sources that females consumed when they perceived little fruit around them. We assumed that males did not do this because empirical data suggest that females consume more protein than males (Uwimbabazi *et al.,* 2021). Thus, when fruit abundance was high, females would eat more fruit alongside males, causing larger parties to form. Environments with a high abundance of fruit in PanWorld represented the refugia bonobos evolved in. Therefore, our results are in line with empirical data that find that bonobos form larger mixed-sex parties than chimpanzees due to inhabiting environments with a higher availability of fruit (White, 1988; White & Wrangham, 1988, Chapman *et al.,* 1994; Furuichi & Hashimoto, 2002; Mulavwa *et al.,* 2008). Patterns of female behavior in PanWorld are in line with patterns of behavior found in nature. Similar to female chimpanzees (Williams *et al.,* 2002), PanWorld females in environments with a low abundance of fruit are mostly solitary and travel less than males. In environments with a high abundance of fruit, similar to female bonobos (Furuichi, 2008; Wakefield, 2008; Wakefield, 2013), PanWorld females spend most of their time in parties. We found that patterns of grouping found in chimpanzees and bonobos may be explained by differences in fruit abundance. This indicates that when chimpanzee and bonobo habitats significantly differed, fruit abundance could have influenced bonobos to form larger mixed-sex parties than chimpanzees.

We found that larger mixed-sex parties emerge without the influence of tumescence. This is in contrast to findings from Surbeck *et al.* (2021), who found that the presence of tumescent females, not an increased food abundance, led to more female attendance in parties. Our study cannot comment on the validity of their findings because tumescence and estrus were not included in our model. Previous theoretical models that included estrus have shown that it can influence grouping in males through self-organization (Te Boekhorst & Hogeweg, 1994a). However, unlike those studies, our model provides novel insight into how ecological factors alone can induce similar patterns, as well as, influence grouping not only in males but also in females.

4.2. Female dominance

In PanWorld, an increase in sociality did not lead to a higher degree of female dominance. We found that FDI was highest in environments with a low abundance of fruit. This was due to an increase in male competition over fruit patches. As males entered more contests, some males gained very high *Dom* values while others developed very low *Dom* values. Thus, a decrease in fruit abundance increased the steepness of the dominance hierarchy and caused many females to rank above males, resulting in a higher degree of female dominance. Similar to previous studies, we show that the frequency of male aggression can significantly influence the degree of female dominance in a population (Hemelrijk *et al.,* 2008; 2017). However, our results contradict the second part of our hypothesis that proposed that an increase in sociality would lead to more contests and a higher degree of female dominance. Importantly, patterns of intersexual dominance in PanWorld do not match empirical studies that find that some female bonobos dominate over males and chimpanzee females do not (Kano, 1992; Parish, 1994; Parish, 1996; Furuichi, 1997; Vervaecke *et al.,* 2000). We found that the degree of female dominance was highest in environments that represented chimpanzees. Bonobo societies can be male-dominated, female-dominated, or co-dominated by both sexes (Paoli *et al.,* 2006). Thus, although our findings are not in line with empirical data on chimpanzees, they do not completely challenge what has been found for bonobos.

Although FDI was highest in environments with a low abundance of fruit, an increase in fruit abundance caused some females to gain very high *Dom* values (close to the highest of the total population). The total number of fights females engaged in significantly decreased with an increase in fruit abundance. However, as females became less solitary they engaged in more male-initiated fights. Males inhabiting environments with a medium and high abundance of fruit initiated more intersexual fights because, on average, they have a higher probability of winning mental battles against females. Females winning male-initiated fights

significantly increases their *Dom* values because males have a larger *StepDom*, and often a higher *Dom* value than females. As females entered more fights that can lead to large increases in rank, the dominance hierarchy of females differentiated more strongly, causing some to gain very high *Dom* values. Interestingly, the steepness of the female dominance hierarchy decreased between environments with a medium and high abundance of fruit. This was because there was less competition over fruit patches, meaning that individuals entered fewer contests. As a result, the female dominance hierarchy differentiated less strongly.

Importantly, patterns of hierarchical steepness in PanWorld do not match those found in empirical data. In PanWorld, the female dominance hierarchy was steeper than the male dominance hierarchy in environments with a medium and high abundance of fruit. Although a steeper female than male hierarchy has been found in some primates (e.g. Kaburu *et al.,* 2012), this finding contradicts research that shows that in captive bonobos, the male hierarchy is steeper than that of females (Stevens *et al.,* 2007). However, the authors did find that steep captive female bonobo hierarchies do arise during periods of intense competition and postulated that wild animals may show different results than captive populations.

4.3. Further research

Our results regarding dominance and interactions elude to the fact that certain patterns of behavior in PanWorld, especially that of males, are not accurate caricatures of chimpanzees and bonobos. Contradicting our hypothesis and previous research, an increase in sociality did not cause individuals to interact more. This was because most fights occurred over access to food patches. We minimized the number of daily interactions by increasing the *Avoidance* parameters during the grouping state. By doing so, we managed to gain a realistic number of daily interactions between individuals, but also limited the effect sociality has on the number of interactions. This is because agents kept a certain amount of distance (larger than *PerSpace*) between them while grouping. As a result, individuals mostly fought over fruit patches, meaning that a higher degree of female dominance emerged in environments with a low abundance of fruit because of intense male competition. We suggest that certain behavioral rules can be added to PanWorld that would alter patterns of behavior regarding interactions and dominance to be more in line with empirical data. Specifically, these behavioral rules would cause an increase in sociality to cause individuals to interact more, reflecting the higher intensity of aggression larger parties induce in nature. Importantly, these additions would not alter patterns of behavior found in PanWorld that currently match empirical data.

We suggest that estrus and rules that enable males to search for females exhibiting tumescence should be added to PanWorld. This is similar to previous chimpanzee models (Te Boekhorst & Hogeweg, 1994a), and we hypothesize that such additions would not significantly affect patterns of behavior that currently match empirical data. An increase in fruit abundance would still lead to a decrease in female solitariness and the formation of larger parties. However, introducing estrus would significantly alter the behavior of PanWorld males and how individuals enter interactions. For example, certain rules could be added that enable males to come into contact with others when searching for females exhibiting estrus, such as by minimizing their *Avoidance* while grouping. We hypothesize that if males prioritize the search for females in estrus, the amount of male-male contests will be highest in environments with a high abundance of fruit. This is because, while searching for females, if females are more social, males would come in contact with each other more often. This would introduce mate competition into the model alongside feeding competition. As a result, we hypothesize that the dominance hierarchy would differentiate more strongly, increasing the degree of female dominance in environments with a high abundance of fruit. Tumescence in PanWorld could also allow for investigations into the effects of pseudo-estrus and bisexuality. Here, the timing of tumescence and who is attracted to them can be manipulated to see how it influences the establishment of a dominance hierarchy. In summary, we hypothesize that adding estrus and sexual attraction to PanWorld could result in patterns of behavior and intersexual dominance that are more in line with empirical data.

Researchers often equate the emergence of female dominance in bonobos to females forming coalitions against males. It is thought that female bonobos are more likely to form coalitions than female chimpanzees

because the increased sociality of bonobos causes females to form stronger social bonds (Parish, 1996; Vervaecke *et al.,* 2000, Stevens *et al.,* 2006). For bonds to form, females have to be near other individuals. In line with previous findings, we show that a closer proximity to party members emerges through self-organization due to an increase in food availability (Wantia *et al.,* 2003). Increased fruit abundance also increased the proportion of peaceful interactions among all individuals, which may support the formation of stronger social bonds. However, it is important to note that female bonobo coalitions are not always indicative of affiliative relationships (Tokuyama & Furuichi, 2016). Coalitions may be related to age, with older females supporting younger females against male aggression (Tokuyama & Furuichi, 2016). Nevertheless, currently in PanWorld, individuals, especially females, are closer to each other in environments with a high abundance of fruit. As a result, we suggest that measuring or adding female coalitions to PanWorld could lead to patterns of behavior more in line with empirical data.

Coalitions can be measured by looking at which individuals attack the same agents within a certain timespan (Hemelrijk & Puga-Gonzalez, 2012). We hypothesize that if female coalitions were measured in PanWorld, the frequency of coalitions against males would correlate with the time that females spend in parties. An interesting addition to PanWorld would be a set of behavioral rules that enable the formation of coalitions. Here, somewhat similar to DomWorld (Hemelrijk, 1999), if agents perceive a fight occurring within a certain distance, they become more likely to engage. Agents can provide support to one of the individuals, possibly based on an affiliative relationship or their dominance values, to skew the outcome of the fight. Individuals might provide support to others because they get something in return, such as access to a fruit patch. By forming coalitions, females can win fights against dominant individuals that they would not beat by themselves. Winning more fights that lead to significant increases in rank could lead to a higher degree of female dominance in the population. As coalitions would be more likely to form in environments with a high abundance of fruit due to the sociality of females, these environments would support the emergence of higher degrees of female dominance. In turn, adding female coalitions to PanWorld could lead to patterns of behavior that are more in line with empirical data and would allow for investigations into the underlying mechanisms of coalition formation in the *Pan* genus.

4.4. Modern *Pans*
We assumed that fruit abundance significantly differed between chimpanzee and bonobo habitats during their initial divergence. Although evidence supports this (Takemoto *et al.,* 2015), many researchers suggest that they do not significantly vary today (Furuichi, 2009). Thus, it remains unclear why patterns of behavior influenced by fruit abundance would persist. It has been proposed that pseudo-estrus in bonobos evolved due to them inhabiting environments with a high abundance of fruit (Furuichi, 2009). As a result, large mixed-sex parties in bonobos persisted even in scarcer environments (Furuichi, 2009; Surbeck *et al.,* 2021). Our results provide some support for this hypothesis. A high consumption of fruits induces and prolongs tumescence outside of estrus in chimpanzees and other primates (Mori et al., 1997; Thompson & Wrangham, 2008). PanWorld females consume the most fruit when fruit abundance is highest. This may indicate that bonobos in refugia were more likely to evolve pseudo-estrus due to their diet. Pseudo-estrus can decrease aggressive male sexual harassment (Surbeck & Hohmann, 2013). This is because males do not need to sexually coerce females if they are perceived as ovulating more often. Pseudo-estrus can also be adaptive by strengthening social bonds between females (Surbeck *et al.,* 2021). Such benefits can lead to more reproductive success, causing pseudo-estrus to be naturally selected. Pseudo-estrus then influences bonobos to form large mixed-sex parties even in less optimal environmental conditions by attracting individuals. Thus, our study provides insight into how an increased fruit abundance could have caused bonobos to form large mixed-sex parties and possibly how these patterns persisted when the environment changed over time.

5. Conclusion
We found that differences in fruit abundance explain patterns of grouping in artificial agents that resemble patterns found in chimpanzees and bonobos. An increased fruit abundance caused females to become more social, leading to the formation of larger mixed-sex parties and the emergence of some females with very high *Dom* values. However, an increase in sociality did not cause a higher degree of female dominance,

contradicting our hypothesis. The degree of female dominance was highest in environments with a low abundance of fruit due to male competition over fruit patches. We argue that such patterns of behavior do not match empirical data, and suggest that adding sexual attraction or female coalitions to PanWorld would result in patterns of behavior that do. Adding tumescence and males that are attracted to them in PanWorld could cause an increase in sociality to influence interactions and intersexual dominance in ways that match empirical data, causing PanWorld males and females to become better caricatures of chimpanzees and bonobos. Similarly, as female dominance in bonobos is often attributed to female coalitions, adding them to PanWorld could lead to patterns of intersexual dominance found in the *Pan* genus. All in all, we found that fruit abundance may explain patterns of grouping found in chimpanzees and bonobos. These species-specific trait differences may dictate why we see differing degrees of female dominance between the two species. With the addition of certain behavioral rules to PanWorld, these claims can be further investigated.

Supplementary materials
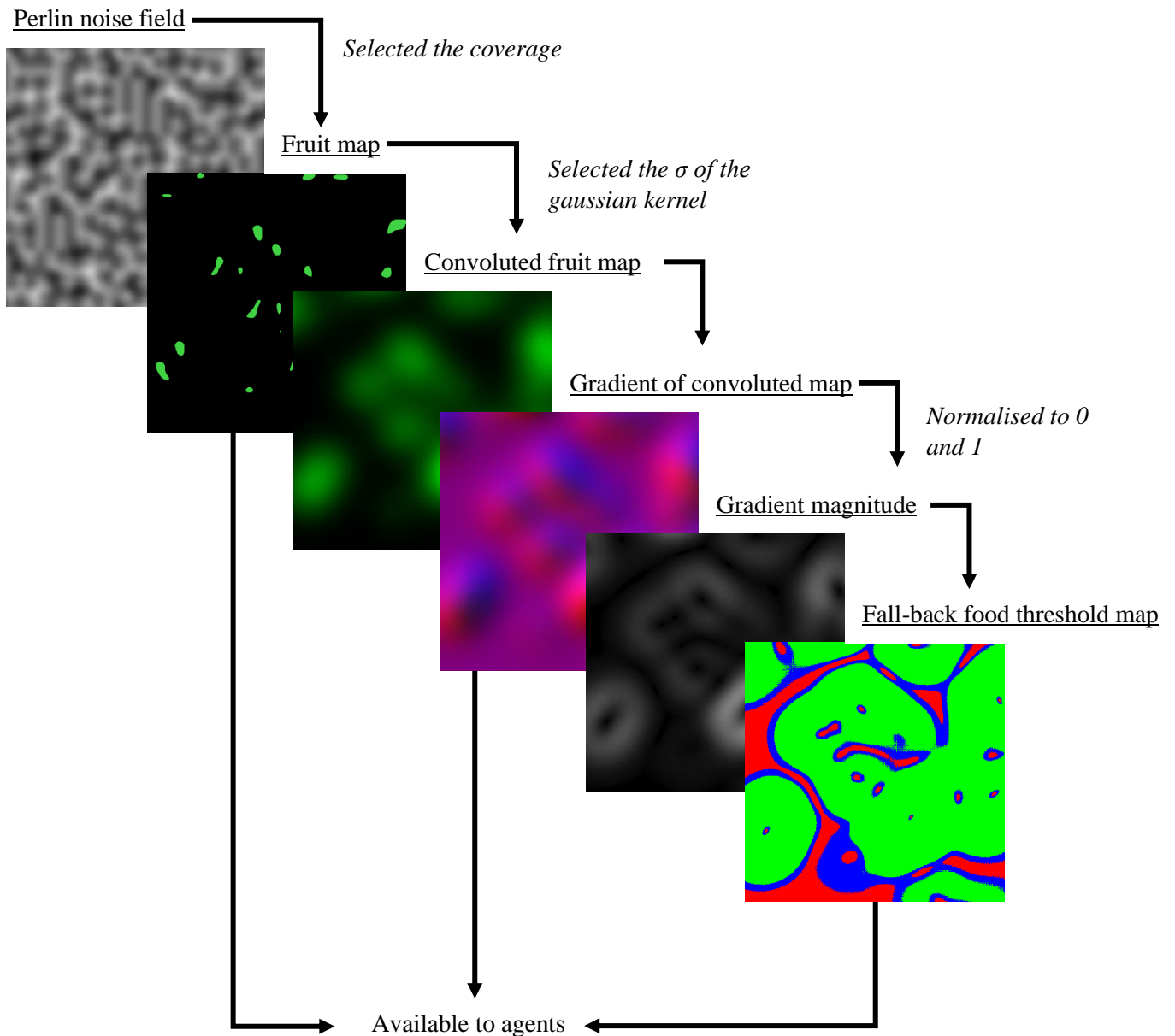
1. Perlin noise

Selected the scale

Figure 1. Schematic representation of how Perlin noise was used to create the PanWorld environment. All composite figures show environments with a low abundance of fruit (1% coverage). Values for the Perlin variables can be found in Supplementary Table 1. Firstly, a *Scale* was chosen for the Perlin noise field. This influenced the distance between fruit patches. Then in order to match the percentage of fruit coverage in the noise field to that found in empirical data, the correct $Clamp_{low}$ for each of the environments was calculated. Noise values below $Clamp_{low}$ were set to 0 and noise values above $Clamp_{low}$ were set to 1. $Clamp_{low}$ was manipulated until the percentage of fruit coverage matched empirical data on the average proportion of fruiting trees in different environments. Agents perceived this binary fruit map as their environment, where 0 represented open space and 1 represented a fruit patch. We then assumed that all of the fruits in the environment released a scent that individuals can perceive. The scent of fruits diffused over the environment. To guide individuals towards patches, the diffusion of fruit scent was created of the convoluted fruit map using a gaussian kernel. We parametrised the σ of the gaussian kernel to match the maximum fruit detection

distance of chimpanzees and bonobos found in empirical data (Janmaat *et al.,* 2013). In the convoluted fruit map figure, the colors correspond to the components of the gradient. *X* values of the gradient vector are mapped as the saturation of blue colors and *Y* values of the gradient are mapped as the saturation of red colors. The normalised gradient was used by individuals as a direction towards fruit patches bearing the most fruit in their close proximity. In the figure, values closer to 1.0 are represented by lighter colors (white) and values closer to 0.0 are represented by darker colors (black). The normalised magnitude of the gradient also influenced what food sources some individuals searched for. This was dictated by A_{low} and A_{high} (Table 1). Females prioritized fall-back foods if the magnitude of the gradient was smaller than A_{low} and prioritized fruits if it was larger than A_{high}. These thresholds are shown in the fall-back food threshold map. Red colors indicate locations where the magnitude of the gradient is smaller than A_{low}, blue colors indicate locations where the magnitude of the gradient is in between A_{low} and A_{high}, and green colors indicate locations where the magnitude of the gradient is larger than A_{high}. To ensure that we can use the same values for A_{low} and A_{high} in each of the three environments, we had to normalise the magnitudes of the gradient. This process led to the calculation of the correct $Grad_{scale}$ required in each of the three environments. The distribution of fruit fluctuates continuously at a slow rate because of Z_{sweep}, which changes the distribution of fruit in our environment. Every second, the *Z* value increased by Z_{sweep}, slightly changing the noise field. When the *Z* value reached a whole number, it was increased by Z_{step}. This ensured that the new distribution of fruit was uncorrelated to the previous distribution, allowing for environmental stochasticity. Iterating over the *Z* value represented fruit depletion, both by individuals and by natural processes, as well as the ripening of fruit on new patches. Thus, the abundance of fruit changed very slightly from one second to the next but averaged out to the selected coverage throughout the simulation.

2. Tables

Table 1. Perlin variables used to create the three environments differing in fruit abundance. Explained in Supplementary Fig. 1.

Variables		Fruit abundance		
		Low	Medium	High
Gaussian kernel	ε	10^{-7}		
	MaxRadius (m)	100.0 m		
	σ^* (m)	15.0 m		
Perlin noise	*Coverage** (%)	1.0 %	7.0 %	13.0 %
	$Clamp_{low}$	0.56	0.40	0.32
	$Grad_{scale}$	153.2	62.2	53.2
	*Scale**	15.0		
	Z_{step}	7.0		
	Z_{sweep}	0.0001		

*variables that were parameterized. Other variables were calculated accordingly.

Table 2. State parameters used to dictate the change of an agent's position. Agent movement and state changes are explained in the main text.

State	Weighting factors for direction vectors					*Avoidance* parameters		*Speed* (m/s)	*Duration* (s)
	w_{prev}	w_{group}	w_{food}	w_{wiggle}	w_{align}	$dist_{avoid}$ (m)	w_{avoid}		
Grouping	10.0	1.0	-0.5	0.5	1.0	10.0	0.005	0.28	n/a
SearchingFruit	1.0	-0.5	1.0	0.5	0.0	1.0	0.5	0.28	n/a
SearchingFBF	1.0	-0.5	0.0	1.0	0.0	1.0	0.5	0.28	n/a
EatingFruit	1.0	0.0	1.0	0.01	0.0	1.0	0.5	0.01	n/a
EatingFBF	1.0	0.0	0.0	0.01	0.0	1.0	0.5	0.001	n/a
Resting	1.0	0.0	0.0	0.01	0.0	1.0	0.5	0.001	300.0
Interacting	1.0	0.0	0.0	0.01	0.0	1.0	0.5	0.01	5.0
Fleeing	1.0	-1.0	-1.0	0.5	0.0	20.0	0.5	0.56	20.0
PeacefulInteraction	1.0	0.0	0.0	0.01	0.0	1.0	0.5	0.01	20.0
RefractoryPeriod	1.0	0.0	0.0	0.01	0.0	1.0	0.5	0.01	20.0

Table 3. Results of comparative statistics (Kruskal-Wallis test and post-hoc pairwise comparison Dunn's test with Bonferroni correction) testing for differences in the diet of PanWorld females and the time spent in different states during the day between environments differing in fruit abundance. Data are based on 20 replicate simulations of each environment.

	Total calories consumed		Amount of FBFs in diet		Time spent solitary		Time spent grouping		Time spent feeding		Number of daily interactions	
Kruskal-Wallis test	H	P	H	P	H	P	H	P	H	P	H	P
	0.00376	0.998	52.5	<0.0001	50.1	<0.0001	52.5	<0.0001	52.5	<0.0001	93.7	<0.0001
Post-hoc Dunn's test (Bonferroni correction)												
Low vs Medium	0.951		0.000879		0.000297		0.000586		0.000586		0.0661	
Low vs High	0.979		<0.0001		<0.0001		<0.0001		<0.0001		<0.0001	
Medium vs High	0.972		0.000879		0.00105		0.000586		0.000586		<0.0001	

Table 4. Results of comparative statistics (Kruskal-Wallis test and post-hoc pairwise comparison Dunn's test with Bonferroni correction) testing for differences in the time spent solitary and in different states during a day between environments differing in fruit abundance for PanWorld males. Data are based on 20 replicate simulations of each environment.

	Time spent solitary		Time spent grouping		Time spent feeding		Number of daily interactions	
Kruskal-Wallis test	H	P	H	P	H	P	H	P
	37.3	<0.0001	50.9	<0.0001	45.1	<0.0001	601	<0.0001
Post-hoc Dunn's test (Bonferroni correction)								
Low vs Medium	0.00178		0.00651		0.00487		<0.0001	
Low vs High	<0.0001		<0.0001		<0.0001		<0.0001	
Medium vs High	0.00545		0.000651		0.000213		<0.0001	

Table 5. Results of comparative statistics (Wilcoxon Signed-Ranks test) testing for differences between PanWorld males and females in the time spent solitary and in different states during the day between environments differing in fruit abundance. Data are based on 20 replicate simulations of each environment.

	Time spent solitary		Time spent grouping		Time spent feeding		Number of daily interactions	
Fruit abundance	*W*	*P*	*W*	*P*	*W*	*P*	*W*	*P*
Low	400	<0.0001	0	<0.0001	400	<0.0001	0	<0.0001
Medium	391	<0.0001	10	<0.0001	393	<0.0001	529	<0.0001
High	345	<0.0001	82	0.00141	324	0.000531	3361	<0.0001

Table 6. Results of comparative statistics (Kruskal-Wallis test and post-hoc pairwise comparison Dunn's test with Bonferroni correction) testing for differences in the proportion of agonistic interactions between different dyads in environments differing in fruit abundance. Data are based on 20 replicate simulations of each environment.

	Dyad							
	Female-Female		Female-Male		Male-Female		Male-Male	
Kruskal-Wallis test	*H*	*P*	*H*	*P*	*H*	*P*	*H*	*P*
	46.3	<0.0001	22.4	<0.0001	40.6	<0.0001	50.9	0.00116
Post-hoc Dunn's test (Bonferroni correction)								
Low vs Medium	<0.0001		<0.0001		<0.0001		0.000383	
Low vs High	<0.0001		0.0259		<0.0001		<0.0001	
Medium vs High	0.00820		0.0249		0.269		0.000664	

Table 7. Results of comparative statistics (Kruskal-Wallis test and post-hoc pairwise comparison Dunn's test with Bonferroni correction) testing for differences in the proportion of peaceful interactions between different dyads in environments differing in fruit abundance. Data are based on 20 replicate simulations of each environment.

	Dyad							
	Female-Female		Female-Male		Male-Female		Male-Male	
Kruskal-Wallis test	*H*	*P*	*H*	*P*	*H*	*P*	*H*	*P*
	36.4	<0.0001	34.5	<0.0001	36.7	<0.0001	40.2	<0.0001
Post-hoc Dunn's test (Bonferroni correction)								
Low vs Medium	<0.0001		<0.0001		<0.0001		<0.0001	
Low vs High	<0.0001		<0.0001		<0.0001		<0.0001	
Medium vs High	0.480		0.480		0.243		0.356	

Table 8. Results of comparative statistics (Kruskal-Wallis test and post-hoc pairwise comparison Dunn's test with Bonferroni correction) testing for differences in the female dominance index and the coefficient of variation of dominance values (steepness) of the population, females, and males between environments differing in fruit abundance. Data are based on 20 replicate simulations of each environment.

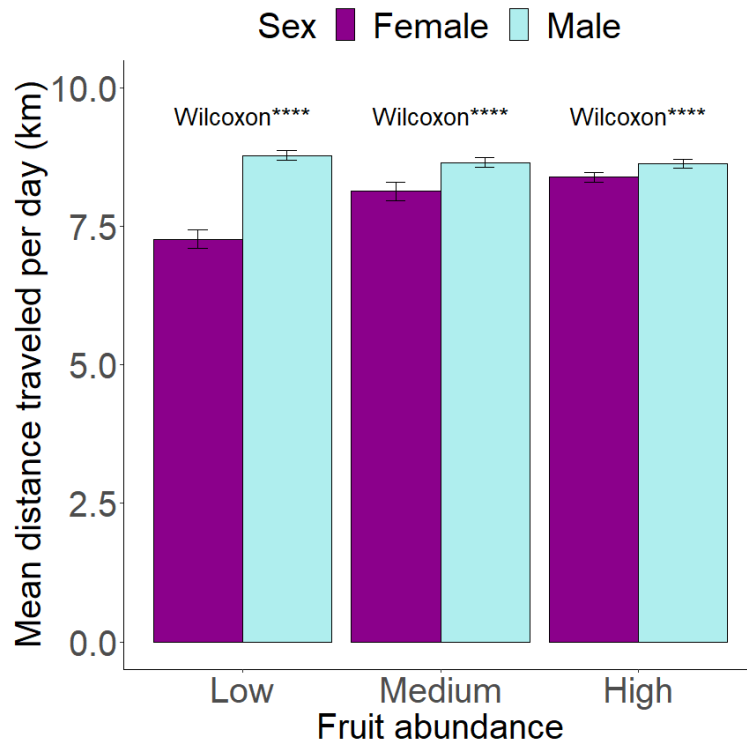|	Female Dominance Index		Population Steepness		Female Steepness		Male Steepness	
Kruskal-Wallis test	*H*	*P*	*H*	*P*	*H*	*P*	*H*	*P*
	38.8	<0.0001	52.2	<0.0001	16.6	0.000252	49.6	<0.0001
Post-hoc Dunn's test (Bonferroni correction)								
Low vs Medium	<0.0001		0.000546		0.000150		0.000257	
Low vs High	<0.0001		<0.0001		0.0838		<0.0001	
Medium vs High	0.762		0.000546		0.0400		0.00135	

3. Figures

Figure 2. The mean daily travel distance by PanWorld females (purple) and males (blue) in environments differing in fruit abundance. Difference amongst replicates indicated by standard deviation. Wilcoxon Signed-Ranks tests found that the distance traveled per day by males and females in each of the environments significantly differed from one another: low ($W = 3$, $P < 0.0001$), medium ($W = 3$, $P < 0.0001$), high ($W = 3$, $P < 0.0001$). A Kruskal-Wallis test found that the differences in daily travel distance for females in each of the environments were significant ($H(2) = 48.488$, $P < 0.0001$). A post-hoc pairwise comparison using Dunn's test indicated that this significant difference was found between each of the environments: low-medium ($P < 0.0001$), low-high ($P = 0.000265$), medium-high ($P = 0.00748$). Similarly, a Kruskal-Wallis test found that the differences in daily travel distance for males in each of the environments were significant ($H(2) = 22.666$, $P < 0.0001$). A post-hoc pairwise comparison using Dunn's test indicated that this significant difference was found between environments with a low and medium ($P < 0.0001$) and low-high ($P = 0.000230$) abundance of fruit but not between environments with a medium and high ($P = 0.625$) abundance of fruit. **** = $P \leq 0.0001$.
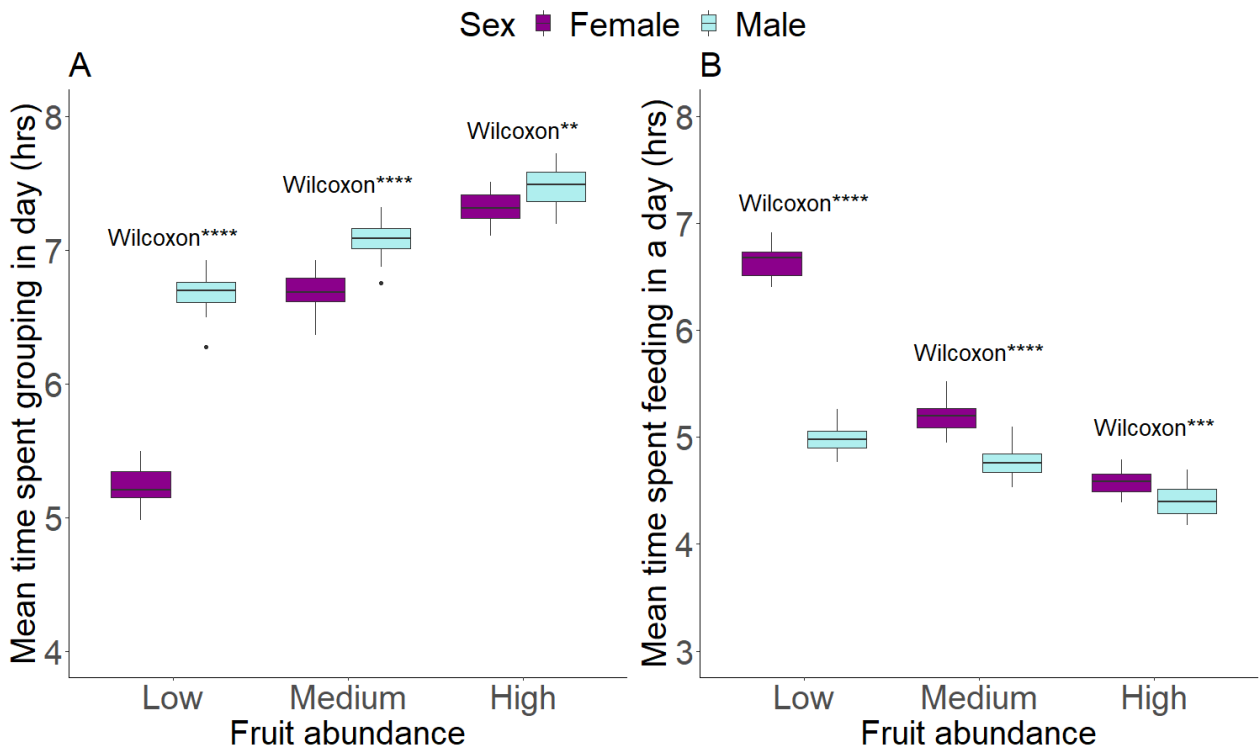
Figure 3. Mean time spent in states associated with grouping (A) and feeding (B) in a day for PanWorld females (purple) and males (blue) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). ** = $P \leq 0.01$, *** = $P \leq 0.001$, and **** = $P \leq 0.0001$. Results of statistical tests are found in Supplementary Tables 3, 4, and 5.
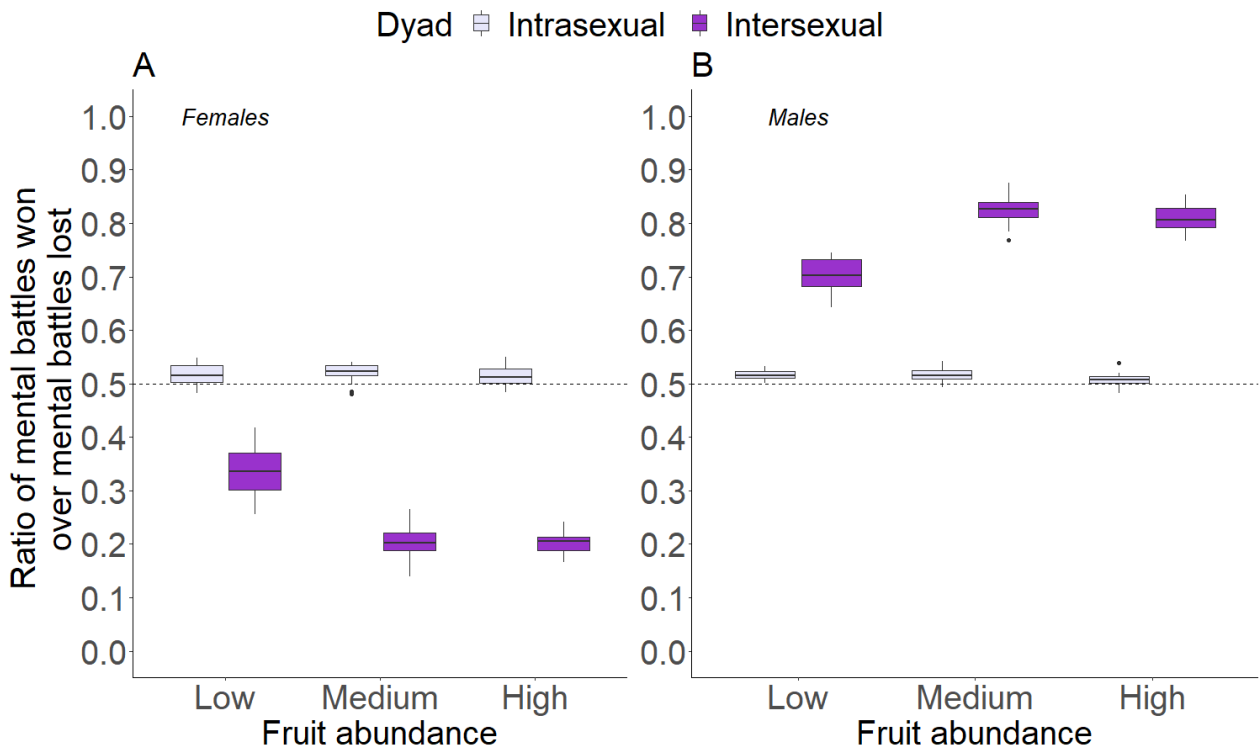
Figure 4. The ratio of intrasexual (light purple) and intersexual (dark purple) mental battles won over mental battles lost by PanWorld females (A) and males (B) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). The dotted line represents a point where *Pans* win half of all their mental battles. A Kruskal-Wallis test found that the differences in the ratio of mental battles won over mental battles lost for females between each of the environments were non-significant for intrasexual dyads ($H(2) = 1.66$, $P = 0.436$) but significant for intersexual dyads ($H(2) = 39.2$, $P < 0.0001$). A post-hoc pairwise comparison using Dunn's test indicated that this non-significant difference for intrasexual dyads was found between each of the environments: low-medium ($P = 0.938$), low-high ($P = 0.938$), medium-high ($P = 0.596$). For intersexual dyads, the significant differences were found between environments with a low and medium ($P < 0.0001$) and low and high ($P < 0.0001$) abundance of fruit but not between environments with a medium and high ($P = 0.921$) abundance of fruit. Similarly, a Kruskal-Wallis test found that the differences in the ratio of mental battles won over mental battles lost for males between each of the environments were significant for intrasexual dyads ($H(2) = 8.02$, $P = 0.0181$) and intersexual dyads ($H(2) = 41.0$, $P < 0.0001$). A post-hoc pairwise comparison using Dunn's test indicated that the significant differences for intrasexual dyads was found between environments with a low and high ($P = 0.0312$) and medium and high ($P = 0.0400$) abundance of fruit but not between environments with a low and medium ($P = 0.814$) abundance of fruit. For intersexual dyads, the significant differences were found between environments with a low and medium ($P < 0.0001$) and low and high ($P < 0.0001$) abundance of fruit but between environments with a medium and high ($P = 0.205$) abundance of fruit.
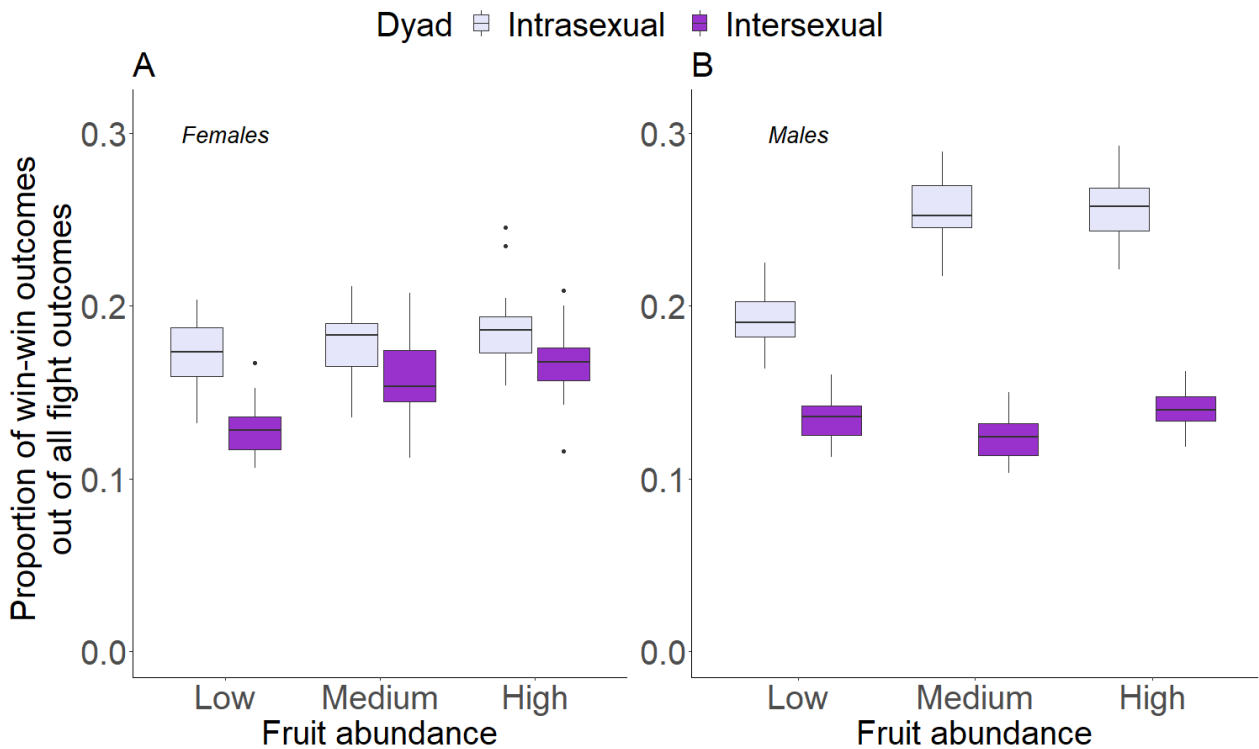
Figure 5. The proportion of intrasexual (light purple) and intersexual (dark purple) win-win outcomes out of all fight outcomes by PanWorld females (A) and males (B) in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). A Kruskal-Wallis test found that the differences in the proportion of win-win outcomes for females between each of the environments were non-significant for intrasexual dyads ($H(2) = 2.75$, $P = 0.275$) but significant for intersexual dyads ($H(2) = 24.5$, $P < 0.0001$). A post-hoc pairwise comparison using Dunn's test indicated that the non-significant difference for intrasexual dyads was found between each of the environments: low-medium ($P = 0.800$), low-high ($P = 0.293$), medium-high ($P = 0.800$). For intersexual dyads, the significant differences were found between environments with a low and medium ($P = 0.00162$) and low and high ($P < 0.0001$) abundance of fruit but not between environments with a medium and high ($P = 0.140$) abundance of fruit. Furthermore, a Kruskal-Wallis test found that the differences in the proportion of win-win outcomes for males between each of the environments were significant for intrasexual dyads ($H(2) = 38.6$, $P < 0.0001$) and intersexual dyads ($H(2) = 11.3$, $P = 0.00345$). A post-hoc pairwise comparison using Dunn's test indicated that the significant differences for intrasexual dyads was found between environments with a low and high ($P < 0.0001$) and medium and high ($P < 0.0001$) abundance of fruit but not between environments with a low and medium ($P = 0.899$) abundance of fruit. For intersexual dyads, the significant differences were found between environments with a low and medium ($P = 0.0363$) and medium and high (P 0.00335) abundance of fruit but not between environments with a low and high ($P = 0.370$) abundance of fruit.
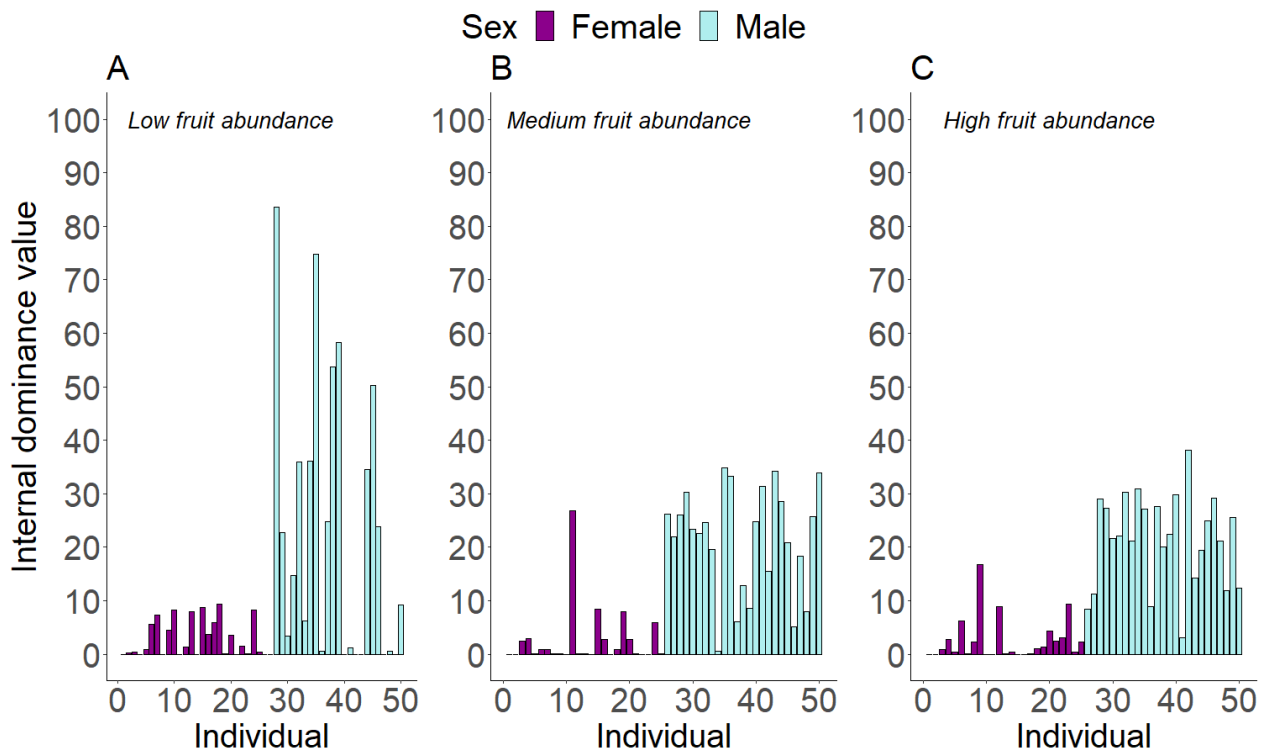
Figure 6. The *Dom* values of all individuals at the end of a simulation in environments with a low (A), medium (B), and high (C) abundance of fruit. Females (purple) are individuals 1 to 24 and males (blue) are individuals 25 to 50. Data taken from random replicates for each of the environments.
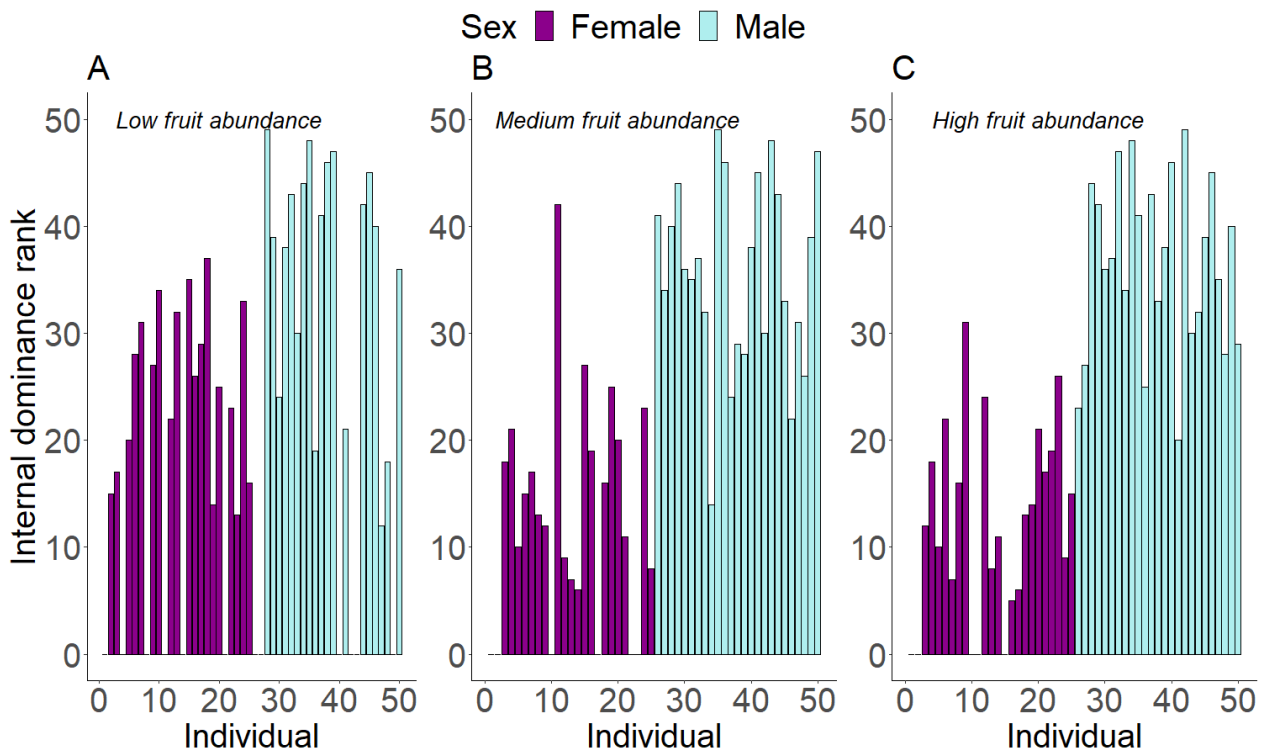
Figure 7. The dominance ranks of all individuals at the end of a simulation in environments with a low (A), medium (B), and high (C) abundance of fruit. Females (purple) are individuals 1 to 24 and males (blue) are individuals 25 to 50. Data taken from random replicates for each of the environments.
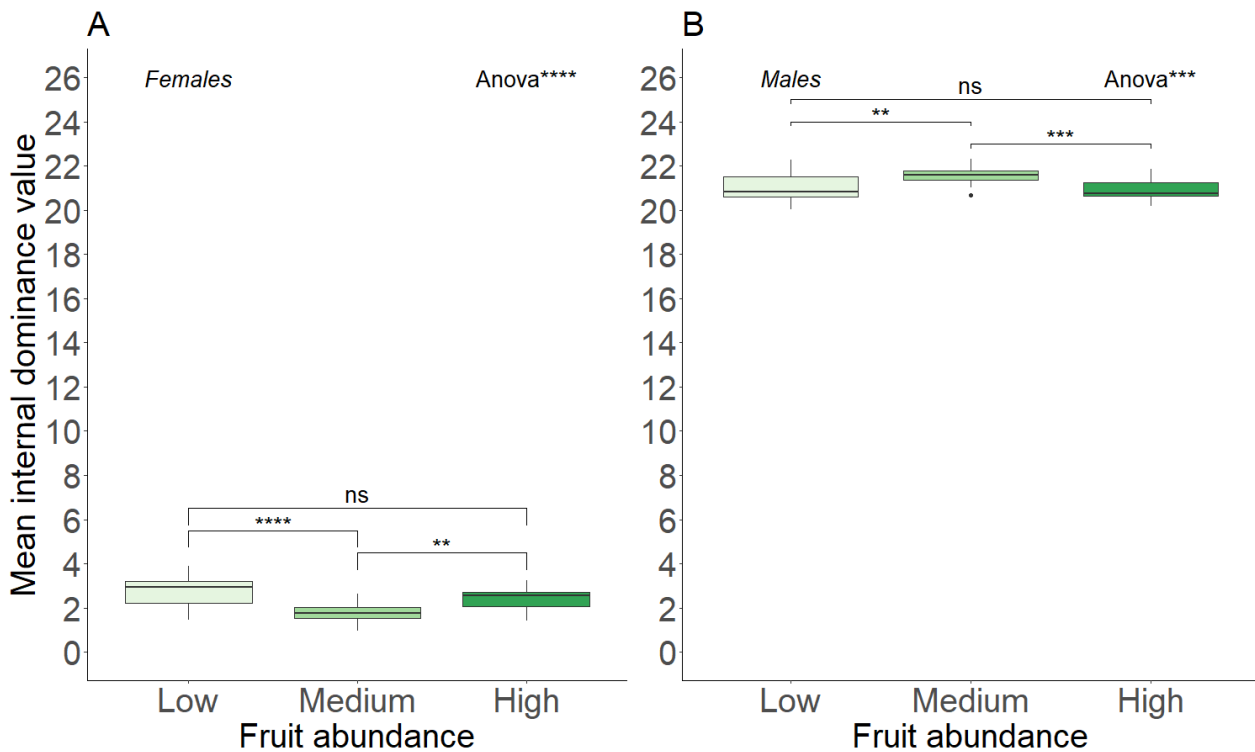
Figure 8. The mean *Dom* values of PanWorld females (A) and males (B) at the end of the simulation in environments differing in fruit abundance. Boxplots show the median (horizontal black line), interquartile range (color filled space), minimum and maximum value, and outliers (black points) of the simulation replicates ($N = 20$). A one-way ANOVA revealed that the differences in the mean dominance values for females between each of the environments were significant ($F(2, 57) = 18.4$, $P < 0.0001$). Tukey's HDS test indicated that the significant difference was found between environments with a low and high ($P < 0.0001$) and medium and high ($P = 0.00167$) abundance of fruit but not between environments with a low and medium ($P = 0.537$) abundance of fruit. A one-way ANOVA also revealed that the differences in the mean dominance values for males between each of the environments were significant ($F(2, 57) = 10.0$, $P = 0.000188$). Tukey's HDS test indicated that the significant difference was found between environments with a low and high ($P = 0.00121$) and medium and high ($P = 0.000546$) abundance of fruit but not between environments with low and medium ($P = 0.966$) abundance of fruit.

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