SOCIAL INSECTS

Lecture 10

Reproductive queueing in primitively eusocial species: predictions and tests

Advanced eusocial:
- morphologically sterile helpers

Primitively eusocial:
- all individuals capable of mating and reproduction

PRIMITIVELY EUSOCIAL

Polistes paper wasp

hover wasp
(stenogastrine)

sweat bee
(halictine)

2cm

Microstigmus wasp

cooperative breeder (scrub-jay)

Small group sizes (often <10)

Reproduction in primitively eusocial wasps

- Reproduction is usually highly skewed towards one 'dominant' individual (e.g. hover wasps)

Hover wasps: Malaysia

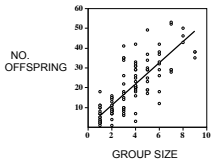
Liostenogaster flavolineata
The hairy-faced hover wasp
"LF"

Liostenogaster flavolineata
(HOVER WASP: STENOGASTRINAE)

- Small nests: ≤ 90 cells
- Initiated by single foundress - lays eggs, feeds developing larvae progressively
- Female offspring have a choice:
  - leave & nest independently
  - become helpers on natal nest: nesting independently has a low payoff
  - groups small (<10 females)

Relatedness in Lf

- Only 1 dominant lays eggs at one time (microsatellites)
- Helpers forage
- $r = 0.52 \pm 0.05$ for adult female nest-mates
  indirect fitness



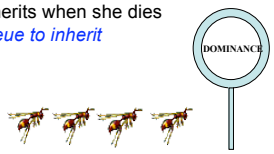
Reproduction in primitively eusocial wasps

- Reproduction is usually highly skewed towards one 'dominant' individual (e.g. 90% in *Lf*)
- But…. when the current dominant dies, another female inherits her position: reproduction is less skewed when viewed across the whole lifespan

What happens when the dominant dies?

Inheritance queue

- Measure all the wasps in many groups: dominants no larger than wasps chosen at random
- Dominant is the oldest female
  Next-oldest inherits when she dies
  Age-based queue to inherit

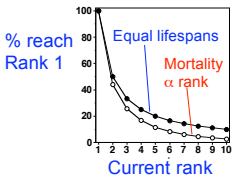


Age-based queues are common….


Stripe-backed wren


Xylocopa carpenter bee

Queueing for inheritance



Queue dynamics
Youngest wasp in group of n

$$P(\text{inherit}) = \frac{\text{expected lifespan}}{\text{expected lifespan} + \text{lifespans of } n\text{-1 older wasps}}$$

Equal lifespans: $P(\text{inherit}) = 1/n$

Inheritance is an important fitness component

Queue to inherit breeding positions

- Consequences of queuing for variation in behaviour between group-members
- Behavioural mechanisms that might stabilize the queue

Variation in behaviour

Individual variation in helping effort

- Meerkat: individuals spend 8-42% time babysitting dom's pups
- Wasps & bees: foraging
  - flight, risk of predation
  - negative correlation with survivorship
  - *Liostenogaster*: 0-100% time spent away from nest (effort measure)

Meerkat (Clutton-Brock et al. 2000)

Liostenogaster flavolineata

Helping effort in wasps

DATE	TIME	YWR	WGG	RYR	WWR
13 Mar	13.00	√	√		√
	13.30		√		√
	14.00	√	√	√	√
	14.30	√			√
	15.00	√			√
	15.30	√	√		√
	16.00		√		√
	16.30	√	√		√
	17.00	√	√		√
14 Mar	13.30	√			√
	14.00				√
	14.30	√	√		√
	15.00	√	√		√
	15.30				√
	16.00			√	√
	16.30	√			√
	17.00	√	√	√	√
16 Mar	13.00	√			√
	13.30	√		√	√
	14.00				√

Genetic relatedness & helping effort

- Predict a correlation between effort and the relatedness of individual helpers to the dominant

Positive correlation:

Negative correlation:

Genetic relatedness & helping effort in vertebrates

- Predict a correlation between effort and relatedness
- Vertebrates: ≈10% variation in effort explained by variation in relatedness (Griffin & West 2003)

Meerkat

Primitively eusocial insects

- Few studies
- In *Lf*, helpers are mainly sisters (r=0.75) or cousins (r=0.1875) of the dominant
- Sisters forage no harder than cousins

Liostenogaster flavolineata

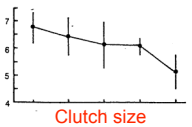
Hamilton's Rule

$rb > c$

c = cost to the altruist
b = benefit to the recipient
r = coefficient of relatedness

Life-history trade-offs: current vs. future reproduction

Clutch size of same parents in year 2



Clutch size (year 1)

Collared flycatcher

Future fitness & helping effort

Trade-off between current & future reproduction

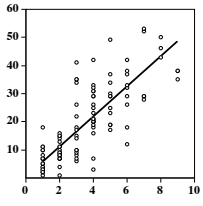
Applied to helpers: trade-off between helping effort & future reproduction

Prediction: individuals with greater future fitness have more to lose, so should work less hard

Index of future fitness = position in queue to inherit. Being nearer the front of queue means more chance of inheriting before you die: higher costs of foraging

Payoff from inheriting the dominant position is larger in a larger group

NO. OFFSPRING



GROUP SIZE

Predictions

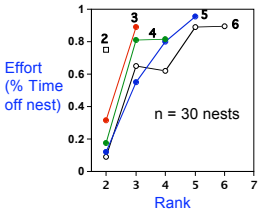
- Helpers nearer to the front of the queue should work less hard
- Helpers of a given rank should work less hard in larger groups: productivity effect
- Age = rank in *Liostenogaster*

Methods

- Wait until the ages (ranks) of the wasps in the queue are known
- Estimate helping effort by each forager: the % time it spent away from the nest foraging
- Estimate relatedness of each helper to the dominant

Predictions

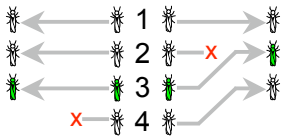
- Helpers nearer to the front of the queue should work less hard
- Helpers of a given rank should work less hard in larger groups: productivity effect



CORRELATION ONLY

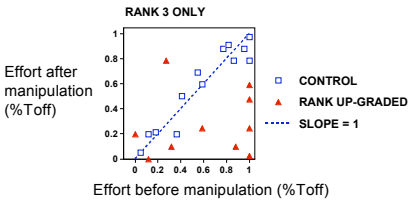
Rank P < 0.001
Group size P < 0.001
Relatedness NS

Manipulate rank



Control R3 promoted

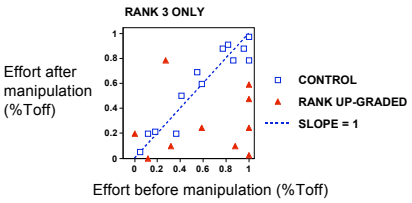
Effort after manipulation:
Control R3>Promoted R3=Control R2



After manipulation:
Effort: Control R3 > Promoted R3 = Control R2
(59%) P=0.01 (28%) (20%)
Age: Control R2 > Promoted R3
(120d) P<0.001 (57d)

Group size and effort

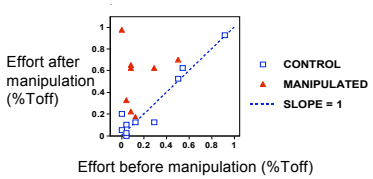
Helpers of a given rank should work harder in smaller groups: stand to inherit less.
Yet……controls don't work harder after manipulation



Group size and effort

- Remove wasps ranked below focal female
- Unmanipulated controls

Effort after manipulation: Manipulated > Control

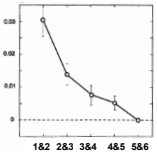


Summary (1)

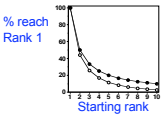
- Considerable individual variation in helping effort in primitively eusocial animals
- Helpers are often in a queue to inherit breeding positions
- Variation in future fitness (chance of inheriting) - may explain a large proportion of the variation in effort and other behaviours

Rates of aggression in *Polistes*

Aggression rate/min. both on the nest



Higher-ranked individuals initiate most aggression



Future fitness may explain variation in behaviours

Kin selection is still important

- In *Lf*, nearly all nest-mates are relatives: helpers are getting indirect fitness
- …but don't fine-tune their effort according to relatedness
- Effort is fine-tunes according to rank and group size.

Queue stability

The queue should be stable

- Each individual would prefer *itself* to be the dominant so that the group rears *its* offspring
- How stable is the queue - are there cheats?

Relative age is a good predictor of inheritance rank

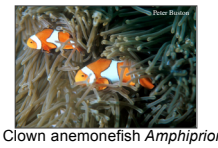
- Experimental removal of dominants (n=70): oldest helper inherits (90%)
- Natural inheritance (n=37): 86% of dominants were the oldest

Queue-jumpers - cheats, or queuing rules more complex?
Relatedness x
Size x
Worked less hard √

What if the rules are broken?

- Only dominant pair breeds
- Queue is size-based: constant size ratio
- Experimental removal: next rank starts to grow
- Each rank restrains its growth so as not to represent a threat
  - manipulate?

(Buston 2003; Heg et al. 2004)



Clown anemonefish *Amphiprion*

Goby *Paragobiodon*

Breaking the rules….

- .
- .
- RESULT: dominant expelled R4 from the group

Goby *Paragobiodon*
Wong et al. (2008)
Current Biology 18: R372-3

Hidden threat of expulsion is revealed only when the rules are broken

Reasons to wait peacefully

- Group-level costs of challenging the dominant?
- Personal cost - expulsion
- Harder to test in wasps

Queue for dominance
Rules unclear
Role reversals

Polistes dominulus
(paper wasp)

Inducing escalated contests

- Remove dominant temporarily
- Allow R2 to establish as new dominant
- Release the old dominant and record her interaction with the R2

Escalated contest results

- Rank 2 immediately submits (n=11)
- Escalated conflict (n=17)
  - R2 submits without injury/expulsion (n=16)
    Original dominant wins 27/28 overall

- By challenging, subordinates *don't* risk expulsion or injury
- *But* the dominant nearly always wins

Do subordinates have any leverage?

- Threaten to leave the group?
- Threat of leaving increased by providing vacant breeding sites
- No effect on reproductive share

Allodapine bee - Langer et al. 2004

Cichlid fish - Heg et al. 2006

Greater threat of leaving didn't enable subordinates to extract a larger share of reproduction

Providing vacant nests


Liostenogaster flavolineata

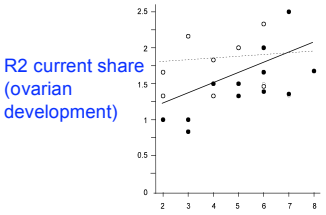
Create vacancies: remove all residents from 39/108 nests

Result negative:
only 6/200 subordinates leave to adopt vacant nests
Leaving may not be a very credible threat

Do subordinates have any leverage?

- Threaten to escalate conflict with the dominant?
- Costly for the dominant
- Dominant could appease subordinate by granting it reproduction
- Predict escalation if subordinate has only a small share of reproduction


Polistes dominulus
(paper wasp)



- more likely to escalate in larger groups ($P<0.02$)
- more likely to escalate if R2 ovaries less developed ($P<0.01$)

By ceding some reproduction, dom could avoid escalation: the threat of escalation could give subordinates leverage

Summary (2)

- A strong relationship between behaviour and queue position suggests that the queue must be reasonably stable
- If the rules are broken, there might be personal as well as group-level costs
- The threat of escalated conflict may allow subordinates to extract reproduction from the dominant