National University of Singapore

LSM1303 Animal Behaviour

Lecture 7: Territoriality

N. Sivasothi aka Otterman

Territory (scope)

- 1. What is territory?
  - 1.1 What does an animal need?
  - 1.2 Home Range vs Territory
  - 1.3 How much is enough?
- 2. Advertisement and defence
  - 2.1 Distant signals – advertisement by scent, sound and visual displays
  - 2.2 Proximal signals – overt displays of aggression, chase & fight
  - 2.3 Maintaining territory: boundary patrols and vigilance
- 3. Why acquire territory?
  - 3.1 Costs
  - 3.2 Benefits of isolation, monopoly and dispersal
  - 3.3. Benefits: Familiarity with environment (home ground advantage)
  - 3.4 Benefits: Familiarity with neighbour
  - 3.5 Is territorial expansion always desirable?
  - 3.6 Inter-specific territoriality or Competition

Territory (scope)

- 4. Do territories ever shrink?
  - 4.1 Tidal territorial compression in Giant Mudskippers
  - 4.2 Natal compression in Smooth-coated Otters
- 5. Why do territory holders *always* win?
  - 5.1 Arbitrary rule hypothesis
  - 5.2 Resource-holding power asymmetry hypothesis
  - 5.3 Payoff asymmetry hypothesis
- 6. Types of territories
  - 6.1. Mating, nesting and feeding
  - 6.2. Mating and nesting
  - 6.3. Mating (lek)
  - 6.4. Nesting
  - 6.5. Feeding territory
  - 6.6. Roosting
  - 6.7. Winter territory
  - 6.8. Deviates

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1. What is territory?

- 1.1 What does an animal need?
- 1.2 Can space be shared?
- 1.3 Home range versus Territory

Sarcastic Fringehead Fights For Territory

Life | BBC Earth (2020) [3:20]

1.1 What resources does an animal need?

What ensures fitness?

- Access to food patches (Foraging)
- Opportunity to find a mate (Courtship & Mating)
- Space to rest and hide

1.1 What resources does an animal need?

- To find food, find a mate, raise young and be protected, space is needed = Home Range
- Must it be exclusive?
- Can animals share a space?
- If the home ranges of different groups of animals overlap, what do animals do? Do they expel or avoid each other?

1.2 Can space be shared?

- Majority of animals share their home range
- Larger and more assertive animals may signal or chase away others if too close
- Most species know to avoid another
- *No direct completion*

Mixed species groups on an African savanna

Mixed-species group of zebras, eland, wildebeest and impala in the Masai Mara. Credit: Jakob Bro-Jør…

Meise, K., Franks, D. W., & Bro-Jørgensen, J. (2020). Alarm communication networks as a driver of community structure in African savannah herbivores. *Ecology letters*, *23*(2), 293-304.

1.1 Shard Home range, with avoidance

Coatis

- solitary males and female groups have a home range (the space they occupy)
- They do not defend a territory
- But avoid overlapping their core area of use
- Omnivore

Also known as "coatimundi"

1.3 Home range versus Territory

What is home range?

- An area in which an animal normally lives (excluding migration)

What is territory?

- An area occupied exclusively by an animal,
- defended by advertisement
- and overt aggression,
- against conspecifics and competitors

How can we tell?

How can we tell?

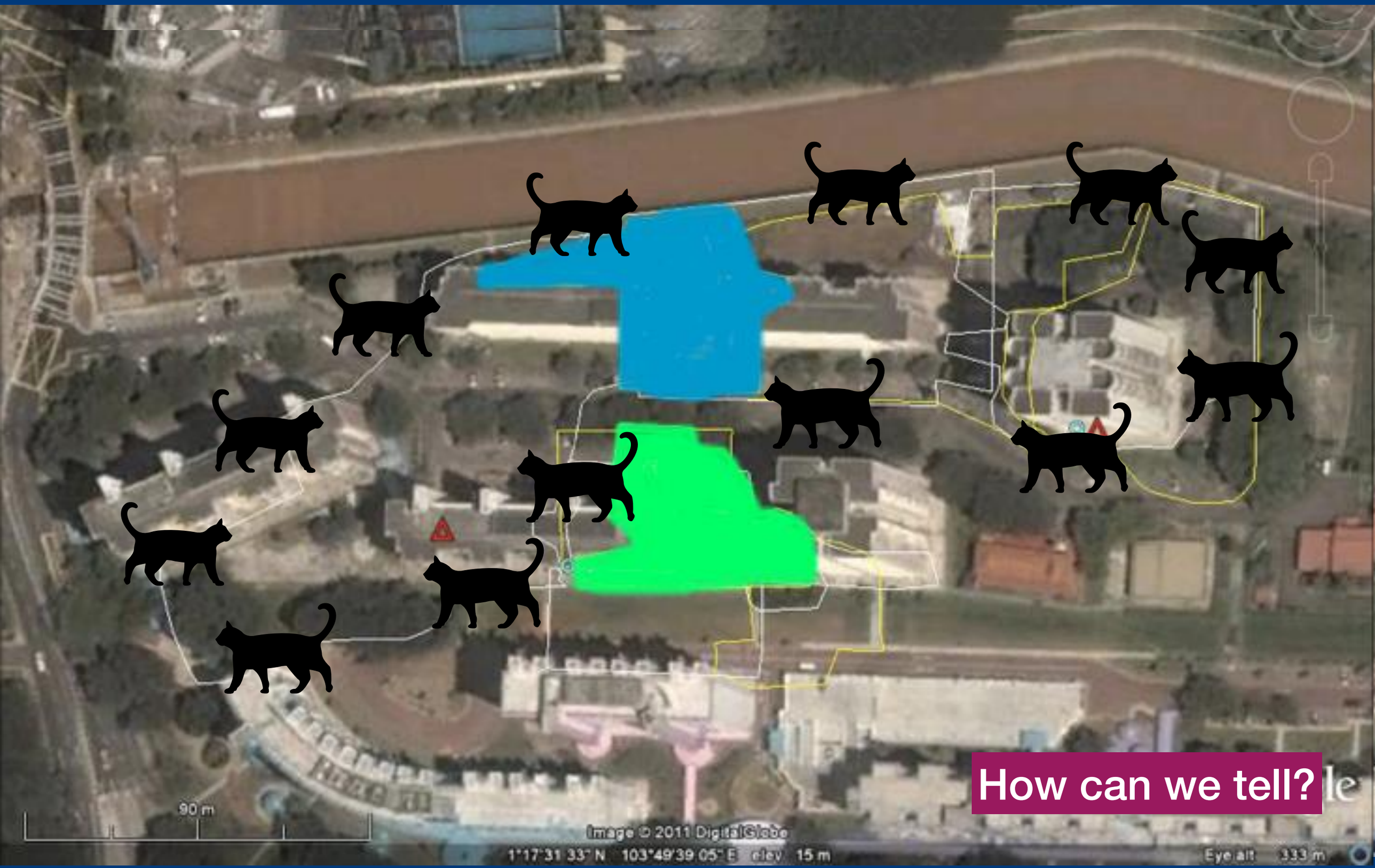
House shrews battling

[Jeff Low, 25 Oct 2021: 32s]

House Shrew (*Suncus murinus*);
photo by Nick Baker (Ecology Asia)

1.3 Home range versus Territory

Home range of sterilised cats in an HDB estate
(Mei Ai Lian (Hons), March 2011)



How can we tell?

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2. Advertisement and defence

- 2.1 Distant signals – advertisement by scent, sound and visual displays
- 2.2 Proximal signals – overt displays of aggression, chase & fight
- 2.3 Maintaining territory: boundary patrols and vigilance

2.1 Distant signals – advertisement by scent (carnivorans)

otter spraints

civet faeces

FUNG Tze Kwan, 2016

2.1 Distant signals – advertisement by scent (carnivorans)

2.1 Distant signals – advertisement by colour (and posture) in the Changeable Lizard, *Calotes versicolor*)

2.1 Distant signals – advertisement by sound, the call of the Collared Kingfisher (*Todiramphus chloris*)

Collared Kingfisher Call - Chinese Gardens, Singapore
Butch in the Bush. YouTube, 23 Feb 2017

2.1 Distant signals – advertisement by sound, the calls of the White-handed Gibbon, *Hylobates lar*

Nick Baker, Ecology Asia

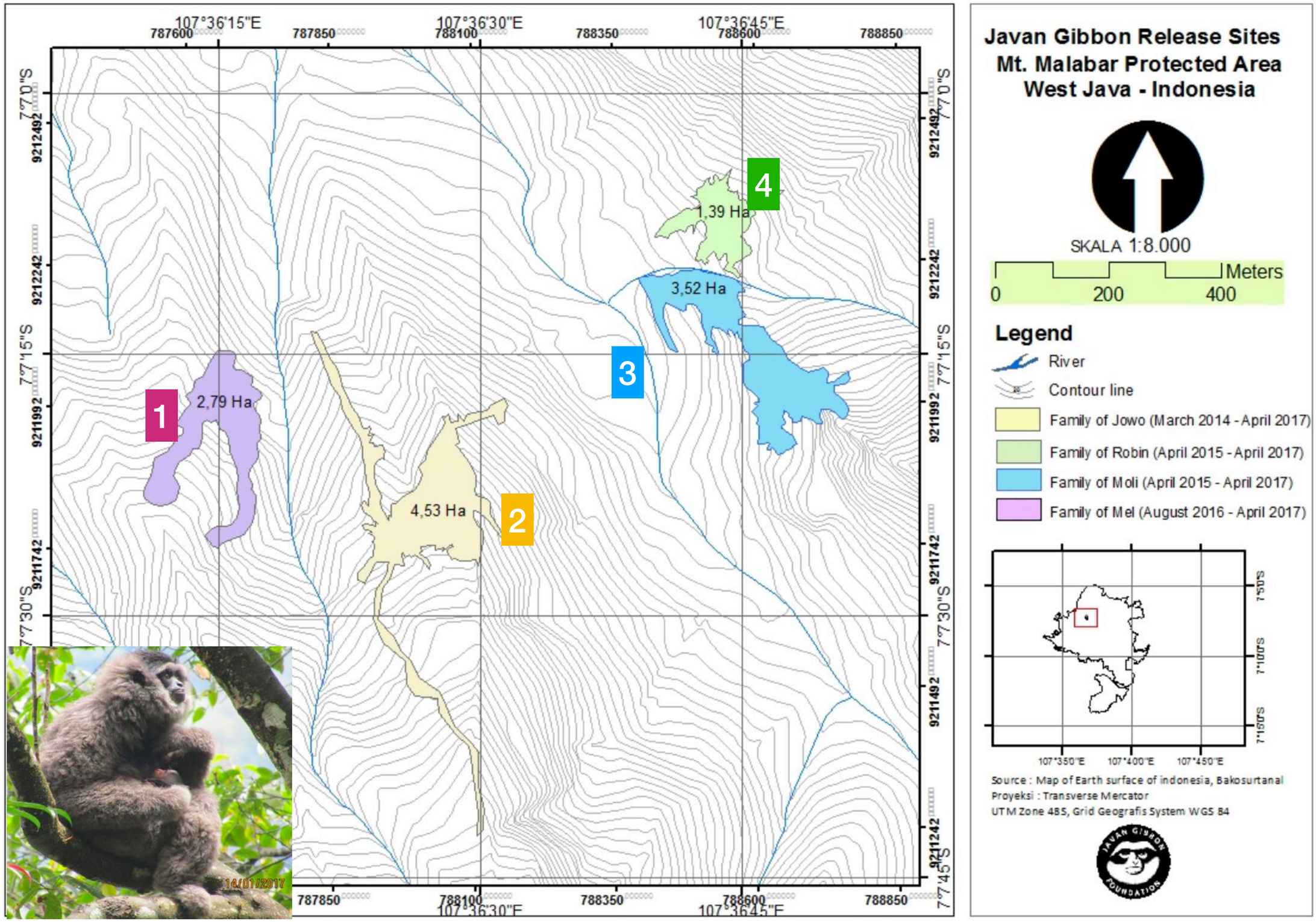


Figure 5. Map of territory sizes of four Java Gibbon group

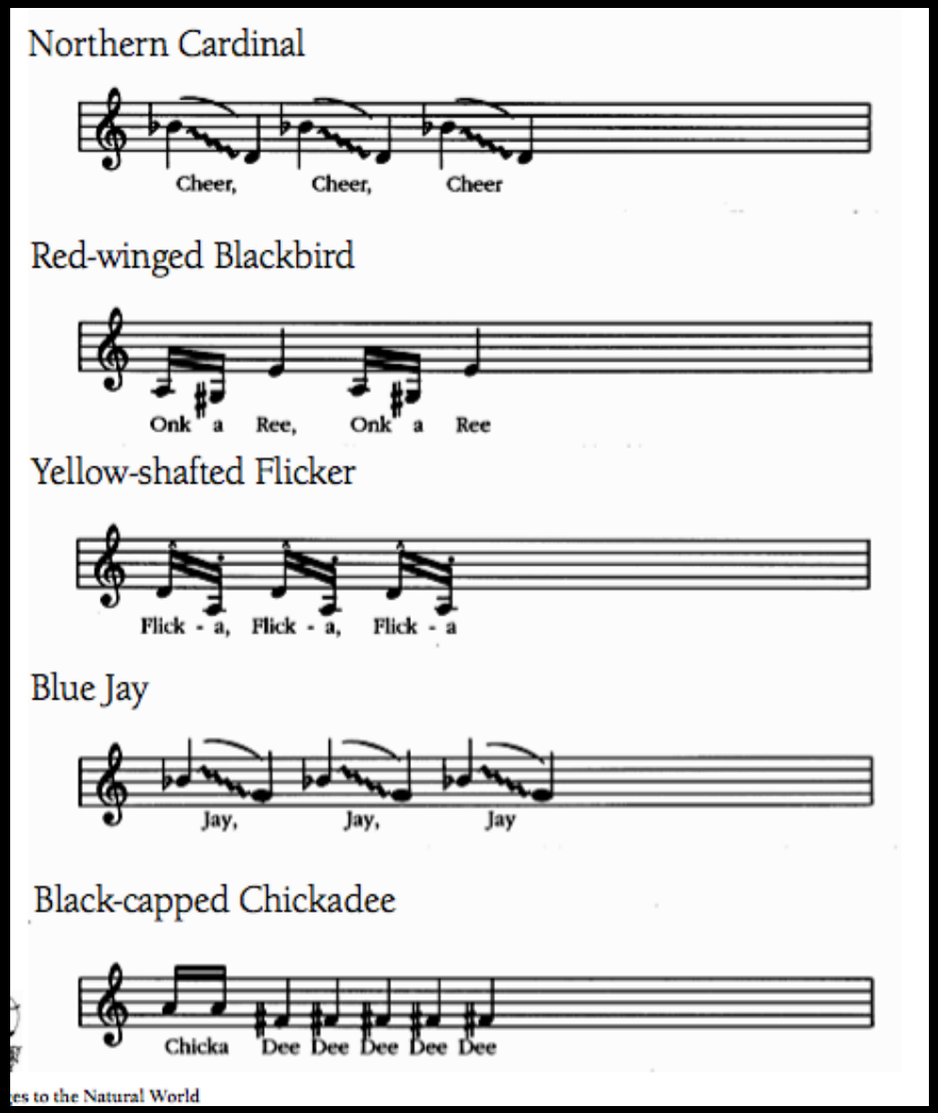
Ario, A., Kartono, A. P., Prasetyo, L. B., & Supriatna, J. (2018). Post-release adaptation of Javan gibbon (*Hylobates moloch*) in Mount Malabar Protected Forest, West Java, Indonesia. *Biodiversitas Journal of Biological Diversity*, *19*(4), 1482-1491.

2.1 Distant signals – advertisement by sound: the dawn chorus of bird songs

Dawn Chorus - a good time to sing!

- Males claim territory, "Go away!" (threaten)
- "Come here!" (entice)
- Listen during gaps
- Females choose a fit mate

2.1 Distant signals – advertisement by sound: the dawn chorus of bird songs

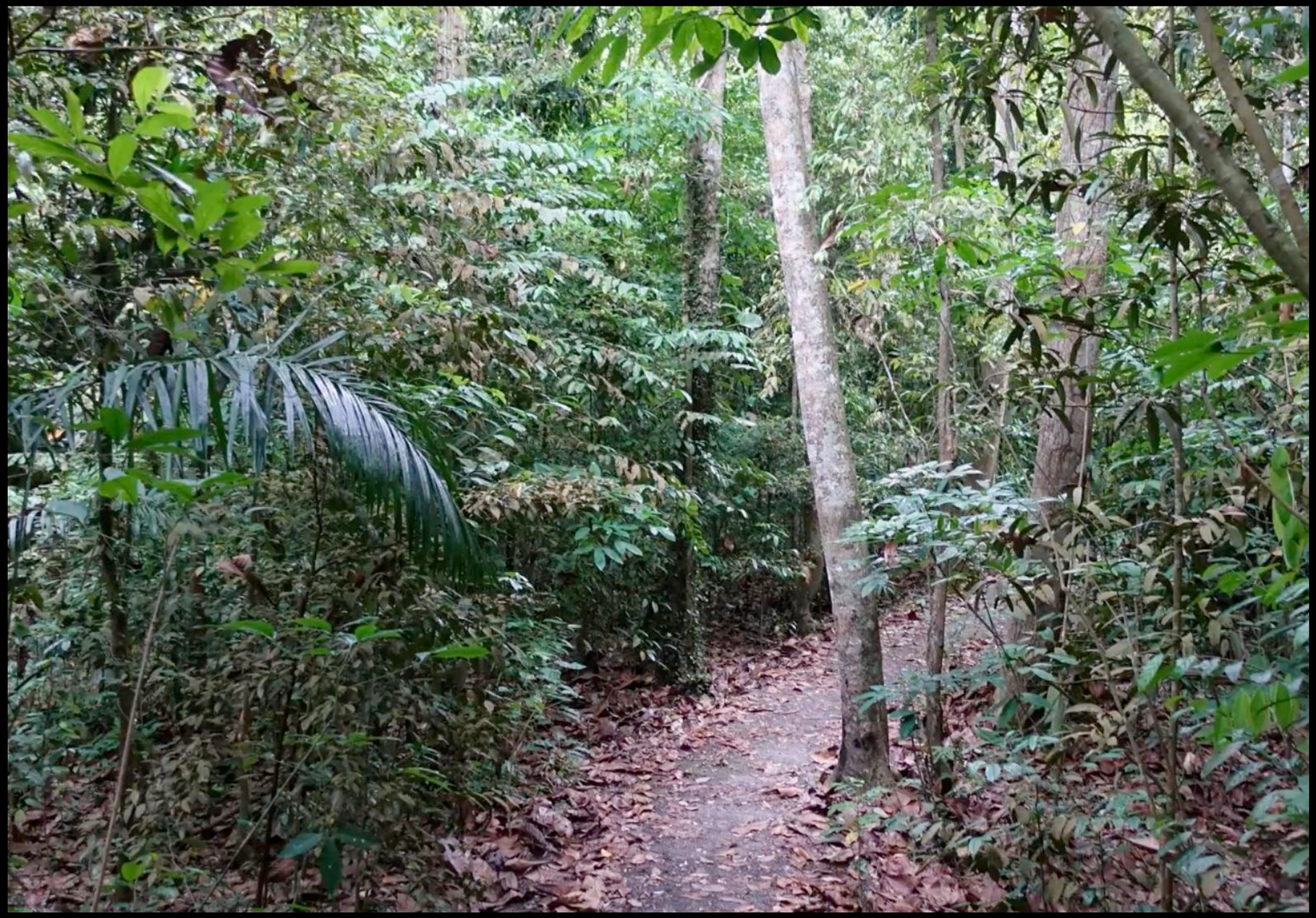


Dawn is a better for sound transmission

An indicator of fitness

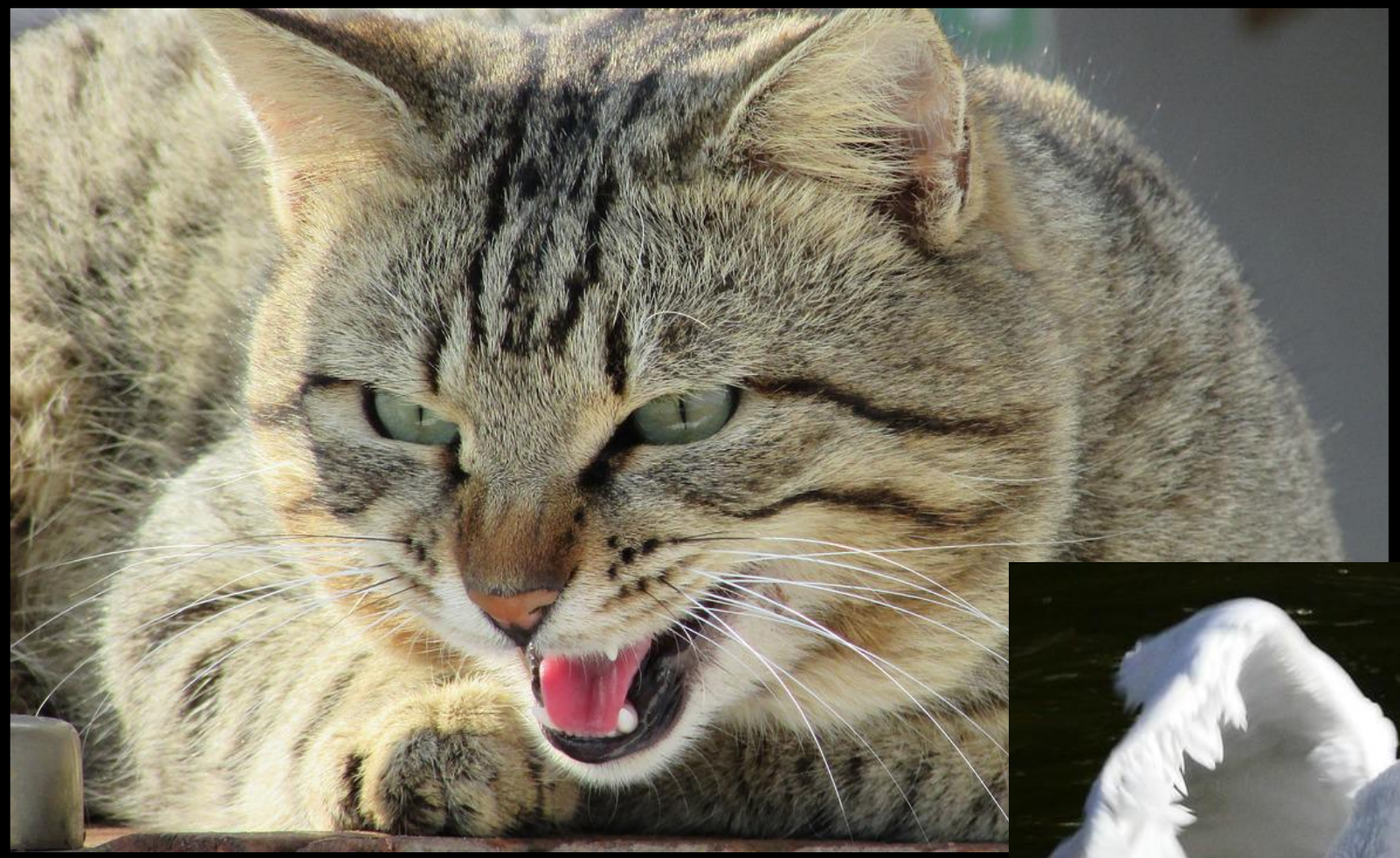
- Males are hungry after a long night, and singing is energy intensive: indicates strength!
- Males may perch to amplify song – become visible and must must evade predators
- Many birds accumulate a repertoire of songs, even borrow from others – complexity indicates survivors of many seasons

2.1 Distant signals – advertisement by sound: the dawn chorus of bird songs

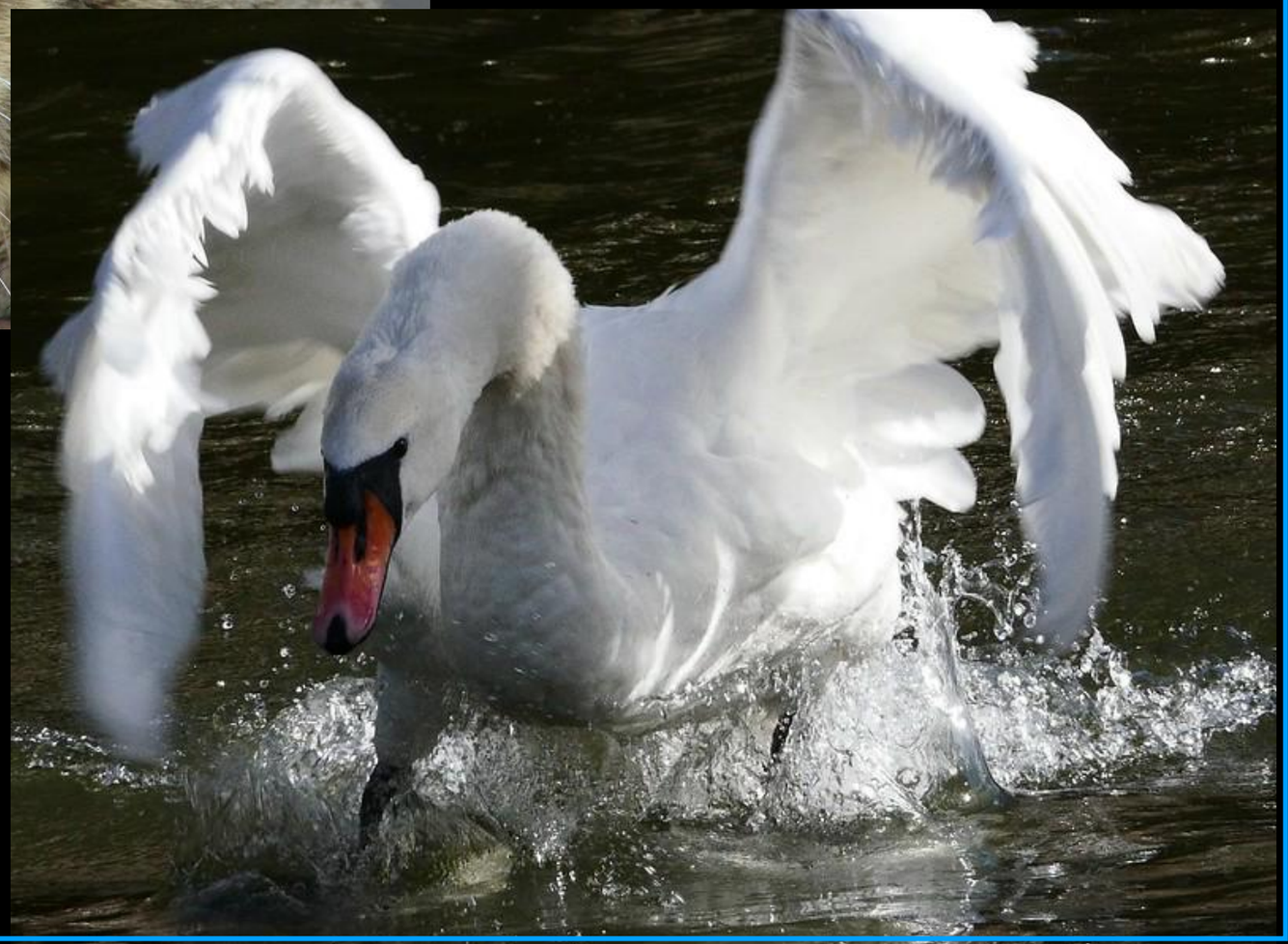


Windsor Nature Park Dawn Chorus
K Kanagasingam, 15 Apr 2018

2.2 Proximal signals – overt displays of aggression, chase & fight



Snarling cat,
needpix.com



Hissing & chasing swan
Shawn Spencer-Smith, Flickr,
26 Mar 2015

2.2 Proximal signals – overt displays of aggression, chase & fight
Smooth-coated otters and dogs (Jeff Teo)

2.2 Proximal signals – overt displays of aggression, chase & fight
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Smooth-coated otters and dogs (Jeff Teo)

2.2 Proximal signals – overt displays of aggression, chase & fight

Territorial fight of Common Sandpipers (*Actitis hypoleucos*)

(Kwong Wai Chong on BESG, 2012)

2.2 Proximal signals – overt displays of aggression, chase & fight

Territorial fight of Common Sandpipers (*Actitis hypoleucos*)

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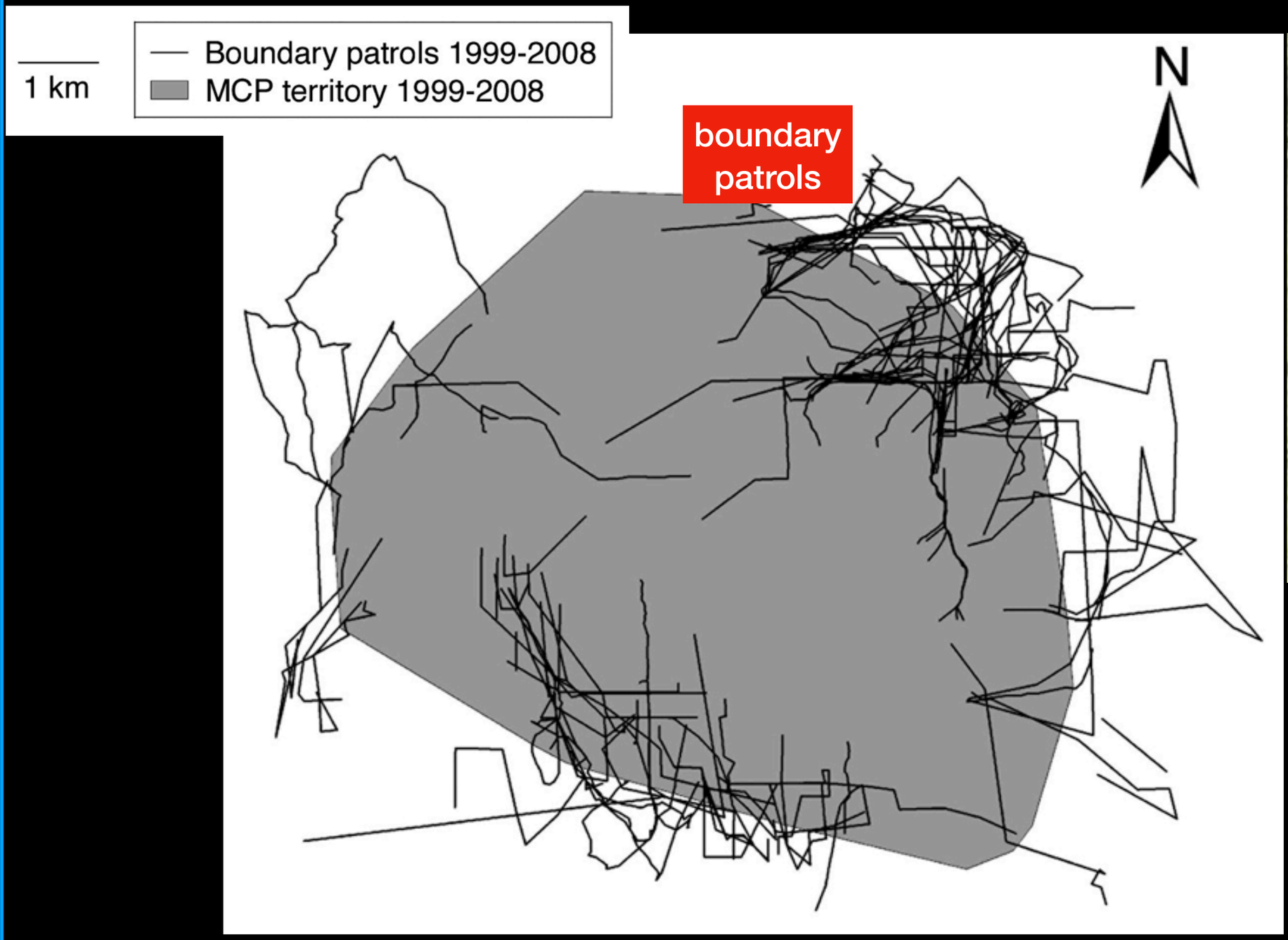
2.2 Proximal signals – overt displays of aggression, chase & fight

Territorial fight of Common Sandpipers (*Actitis hypoleucos*)

(Kwong Wai Chong on BESG, 2012)

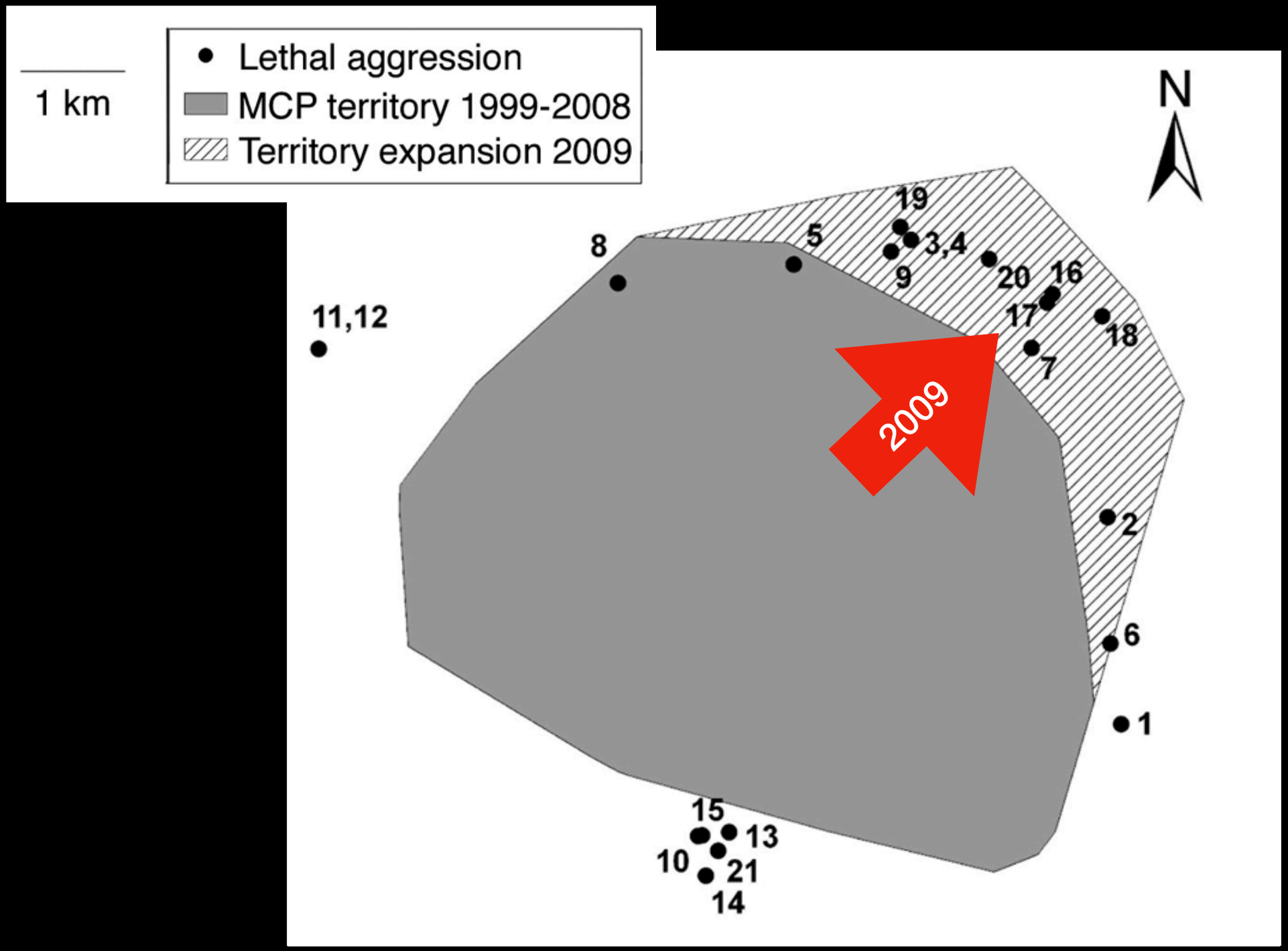
BIRD ECOLOGY STUDY GROUP

2.3 Maintaining territory: boundary patrols and vigilance
Intergroup aggression chimpanzees



Mitani, J. C., Watts, D. P., & Amsler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Current biology, 20(12), R507-R508.

2.3 Maintaining territory: boundary patrols and vigilance
Intergroup aggression chimpanzees



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BBC's Planet Earth: Chimpanzee Patrol

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3. Why acquire territory?

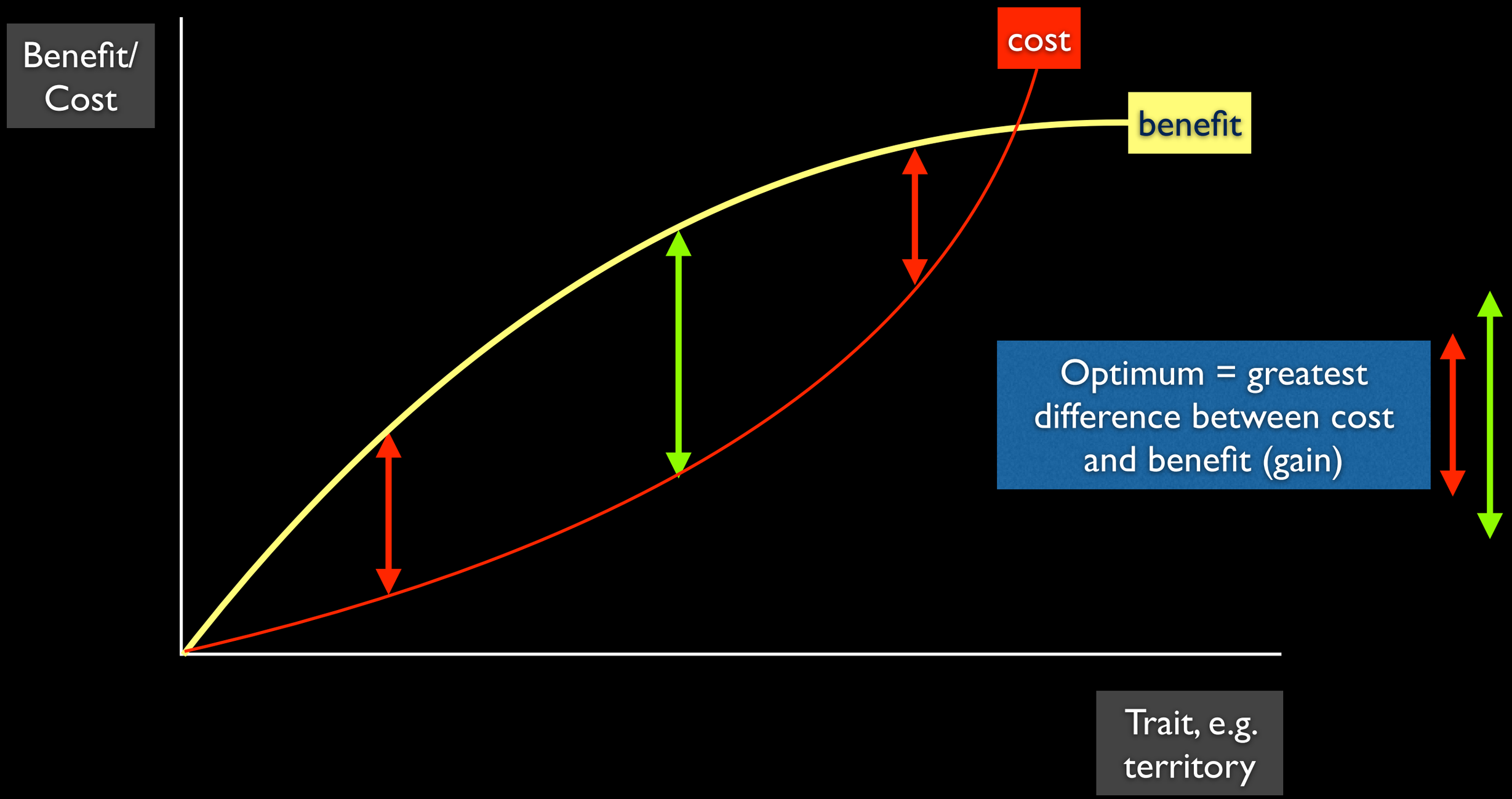
- 3.1 Costs
- 3.2 Benefits of isolation, monopoly and distribution (space)
- 3.3. Benefits: Familiarity with environment (home ground advantage)
- 3.4 Benefits: Familiarity with neighbour
- 3.5 Is territorial expansion always desirable?

3. Why acquire territory?

Optimality: Benefits > Costs = fitness

- Organisms interact to obtain resources, exhibiting a range of behaviours from antagonism to cooperation
- Interactions are costly: energy is required
- Even avoidance is costly if energy is expended but no resource is obtained
- Energy spent is a cost, and the resources gained are benefits.

Optimality = maximise gain (or payoff)



Why acquire territory:
3.1 Costs

- Search and Acquisition require energy and time,
- The animal may go hungry, suffer from injury navigating terrain or from encounters with territorial animals or predators

Cost of dispersal in urban environment: smooth-coated otter killed at West Coast Park, 19 May 2011

Why acquire territory: 3.1 Costs

- Once territory is acquired, it requires
  - constant advertisement
  - and vigilance by patrolling
- Ritualised combat evolved as it reduces costs of combative encounters for mates and territory, as contestants avoid severe harm.

Why acquire territory?
3.2 Benefit: Isolation from others of its kind

1. Reduced the dangers and disadvantages of crowding
   e.g. interference during courtship, pairing, sex, rearing of young.

2. Monopoly of food and nesting materials
   (resources last longer, less depleted).

3. Fighting reduced, energy saved

4. Reduced promiscuity (multiple matings), family stable

5. Ownership is a stimulant for breeding

Why acquire territory?
3.2. Benefits of monopoly and distribution (space)

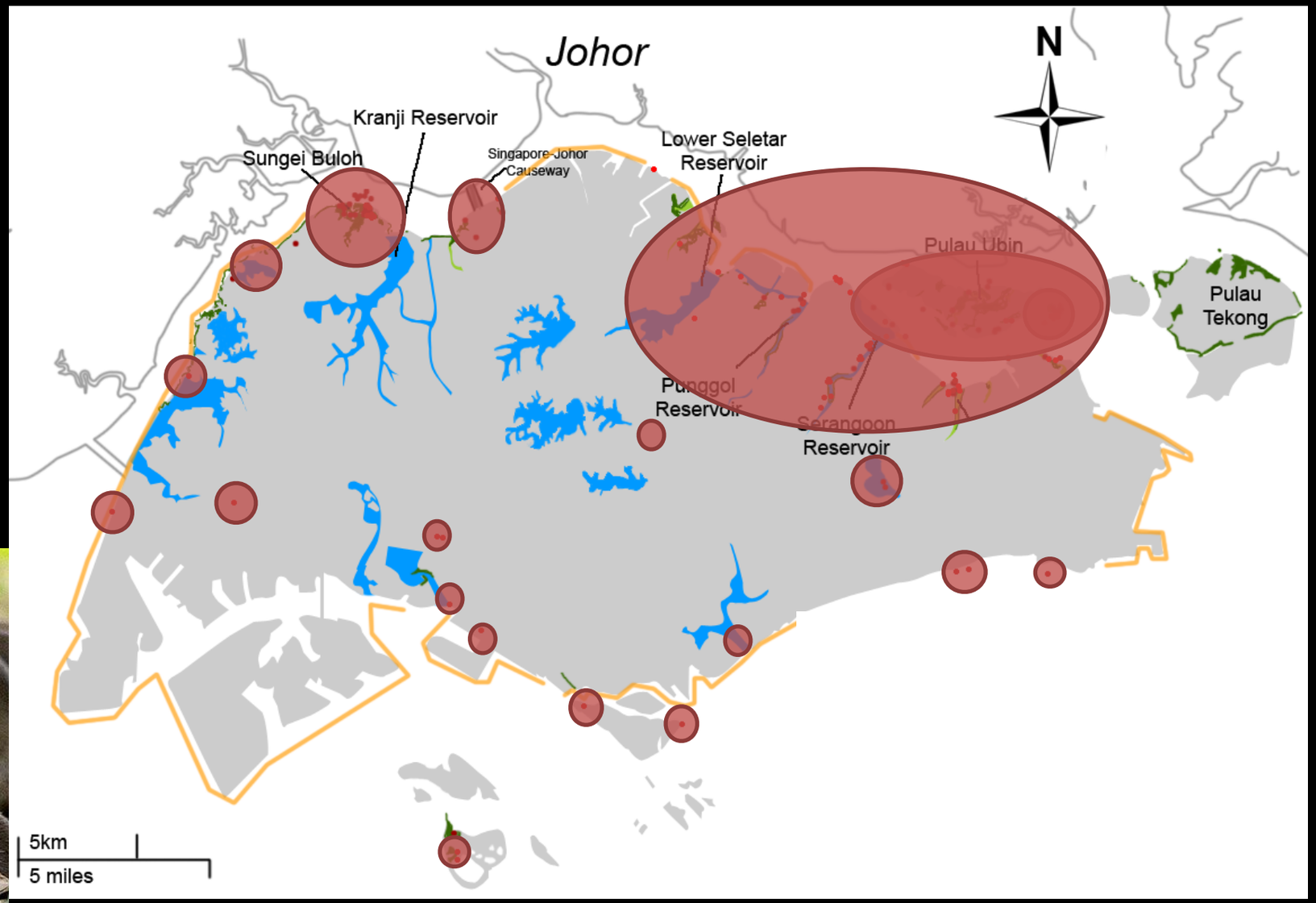
1. Promotes the efficient exploitation resources (e.g. food, nest sites).

2. Reduction of incidence of disease

3. Increases difficulty of predation with widely distributed individuals

4. Parental preparation for next brood easier once previous young leaves nest

2015 – multiple resident, territorial, breeding populations of smooth-coated otters in Singapore: dispersed



2015 (SG50) Bishan Family

Why acquire territory?
3.3. Benefits: Familiarity with environment (home ground advantage)

1. Resident knows where to find food

2. Resident knows the best escape routes

3. Resident knows where to find nest materials, etc.

E.g. Deer mice and the Screech owl

Screech
owl

Deer mice

"Phototrap Model 33 Kit",
Naturefriend magazine

Why acquire territory?

3.3. Benefits: Familiarity with environment (home ground advantage): predator avoidance

- E.g. Deer mice and Screech owl
- Two mice exposed simultaneously (2-30 min) each time;
- One resident and one transient, 20x
- Owls captured few residents (2), and many unfamiliar transients (11)

Why acquire territory?
3.4 Benefits: Familiarity with neighbour

- The "Dear enemy" effect – being less aggressive towards neighbours
- Maintained by "tit for tat"

Ninahale, Wikipedia.
Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

Why acquire territory?
3.4 Benefits: Familiarity with neighbour

Territoriality can foster cooperative bonds between neighbours

- Initial cost – neighbours compete and set up territorial boundaries
- There is stability after this "negotiation" and subsequently a reduced response to neighbours (great benefit over the long-term)

Ninahale, Wikipedia. Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

Why acquire territory?
3.4 Benefits: Familiarity with neighbour

A new neighbour is costly

- Must renegotiate with a stranger
- Costs time and energy, have to re-invest the cost and risk
- Thus, it is less aggressive to neighbours than to strangers
- This is the "dear enemy" effect

Ninahale, Wikipedia. Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

Why acquire territory?
3.4 Benefits: Familiarity with neighbour

The dear enemy effect has been demonstrated in other animals, such as ants!

Langen, T.A., F. Tripet, P. Nonacs, 2000. The red and the black: habituation and the dear-enemy phenomenon in two desert Pheidole ants. Behavioral Ecology and Sociobiology 48 (4): 285-292.

Major *Pheidole* sp. worker from Danum Valley, Sabah, Malaysia. Photo by Steve Shattuck.

Why acquire territory?
3.4 Benefits: Familiarity with neighbour

The "dear enemy effect" is stable only when the reduced aggression is reciprocal,

- i.e. the neighbour cooperates by respecting territorial boundaries
- If a neighbour trespasses, the resident will exhibit heightened aggression, i.e. "tit for tat"

Ninahale, Wikipedia. Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

Why acquire territory?
3.4 Benefits: Familiarity with neighbour:
"Tit for tat" maintains the relationship

In an experiment, a neighbour's call was played back deep in the resident's territory

- Result? *Heightened aggression* displayed by male territory owners towards neighbours, i.e. "tit for tat"
- But this heightened aggression was not maintain when the stimulus was stopped

Ninahale, Wikipedia. Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

Hyman, J. (2002). Conditional strategies in territorial defense: do Carolina wrens play tit-for-tat? Behavioral Ecology Vol. 13 No. 5: 664-669

3.5 Is territorial expansion always desirable?

Does a neighbour limit territory?

- If a neighbour is removed,
- would there be an increase in territory size of the adjacent resident?

Ninahale, Wikipedia.
Yucatan Peninsula,
Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

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3.5 Is territorial expansion always desirable?

Does a neighbour limit territory?

- If a neighbour is removed,
- would there be an increase in territory size of the adjacent resident? NO (expt.)
- Cost of expansion must have been too high – expansion of territory has a cost

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Yucatan Peninsula,
Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

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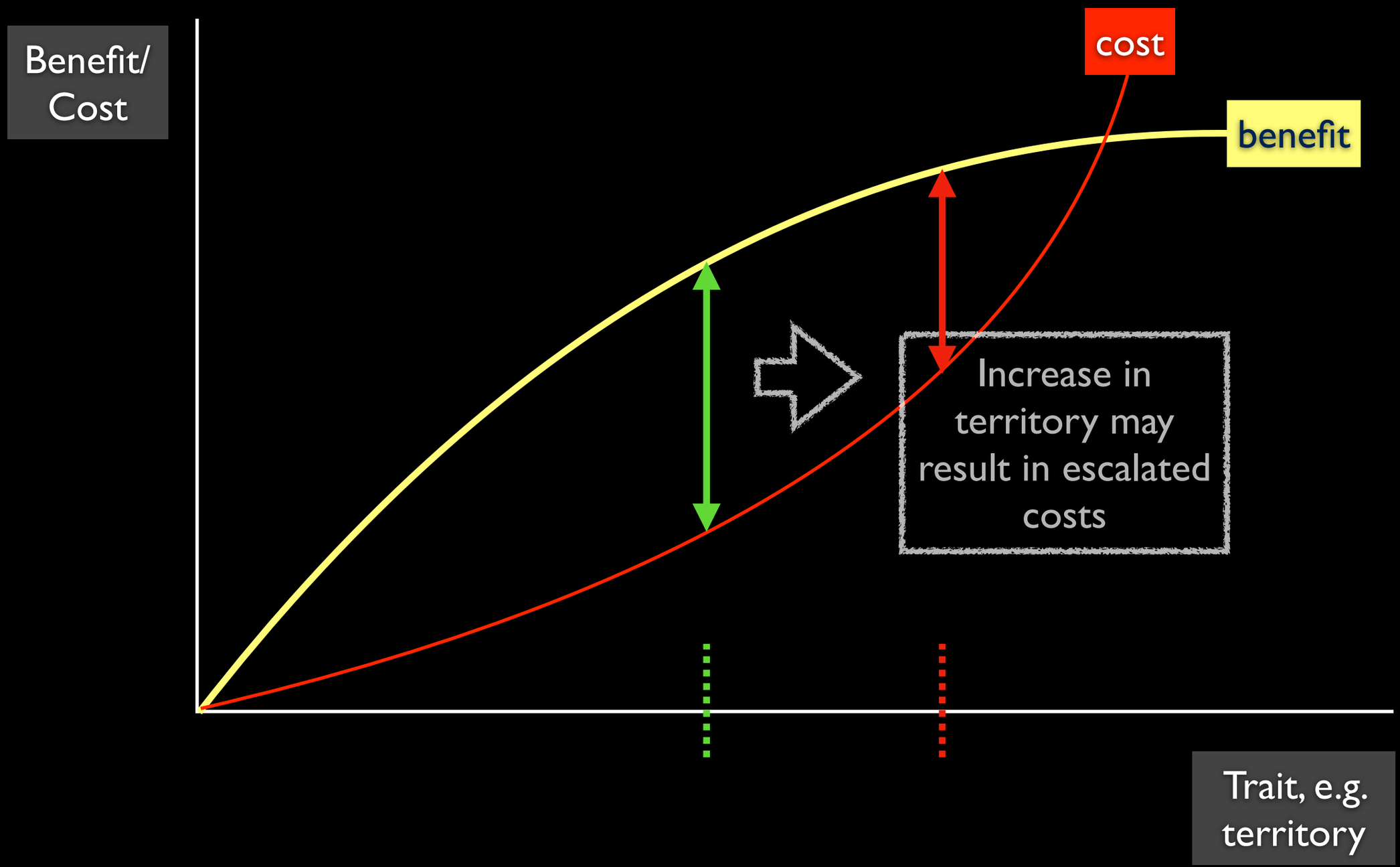
Optimality = maximise gain (or payoff)



3.5 Is territorial expansion always desirable?

A stable neighbour ("dear enemy") has *benefits*

- Reduced fighting
- Form a defensive coalition
- Avoid attracting intruders

Ninahale, Wikipedia.
Yucatan Peninsula, Mexico

Godard, R. (1993). Tit for tat among neighboring hooded warblers. Behavioral Ecology and Sociobiology, 33(1), 45-50.

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3.6 Inter-specific territoriality or competition: what determines the outcome of battles?

Eternal Enemies

(Beverly & Dereck Joubert, National Geographic)

Competition between carnivores in Africa

- Average carnivore in Africa shares some of its geographic range and habitat with 26 other species.
- Carnivores may have to share food resources with 22 other carnivore species, on average.
- The average African carnivore may be vulnerable to predation by 15 other species (although unlikely to be eaten by other carnivores).

Caro, T. M., & Stoner, C. J. (2003). The potential for interspecific competition among African carnivores. Biological Conservation, 110(1), 67-75.

Shared territories leads to greater competition

“Eternal Enemies”

(Beverly & Dereck Joubert, National Geographic, 3:43)

3.7 Inter-specific territoriality or competition: the specific role of male lions and female hyaenas

Maintain territory by eliminating competition

Eternal Enemies

(Beverly & Dereck Joubert, National Geographic, 4:30)

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4. Do territories ever shrink?

- 4.1 Tidal territorial compression in Giant Mudskippers
- 4.2 Natal compression in Smooth-coated Otters

4.1 Tidal territorial compression in Giant Mudskippers

Mudskipper burrows are widely separated from each other as the result of territorial behaviour

sbwr05jun2008-141

Burrows are maintained and defended by male mudskippers

Fish uses 'water tongue' to grab prey on land

Mudskipper feeding system offers an explanation for how early animals adapted to land.

Daniel Cressey, 18 March 2015

Mudskipper move out of their burrows in order to search for food

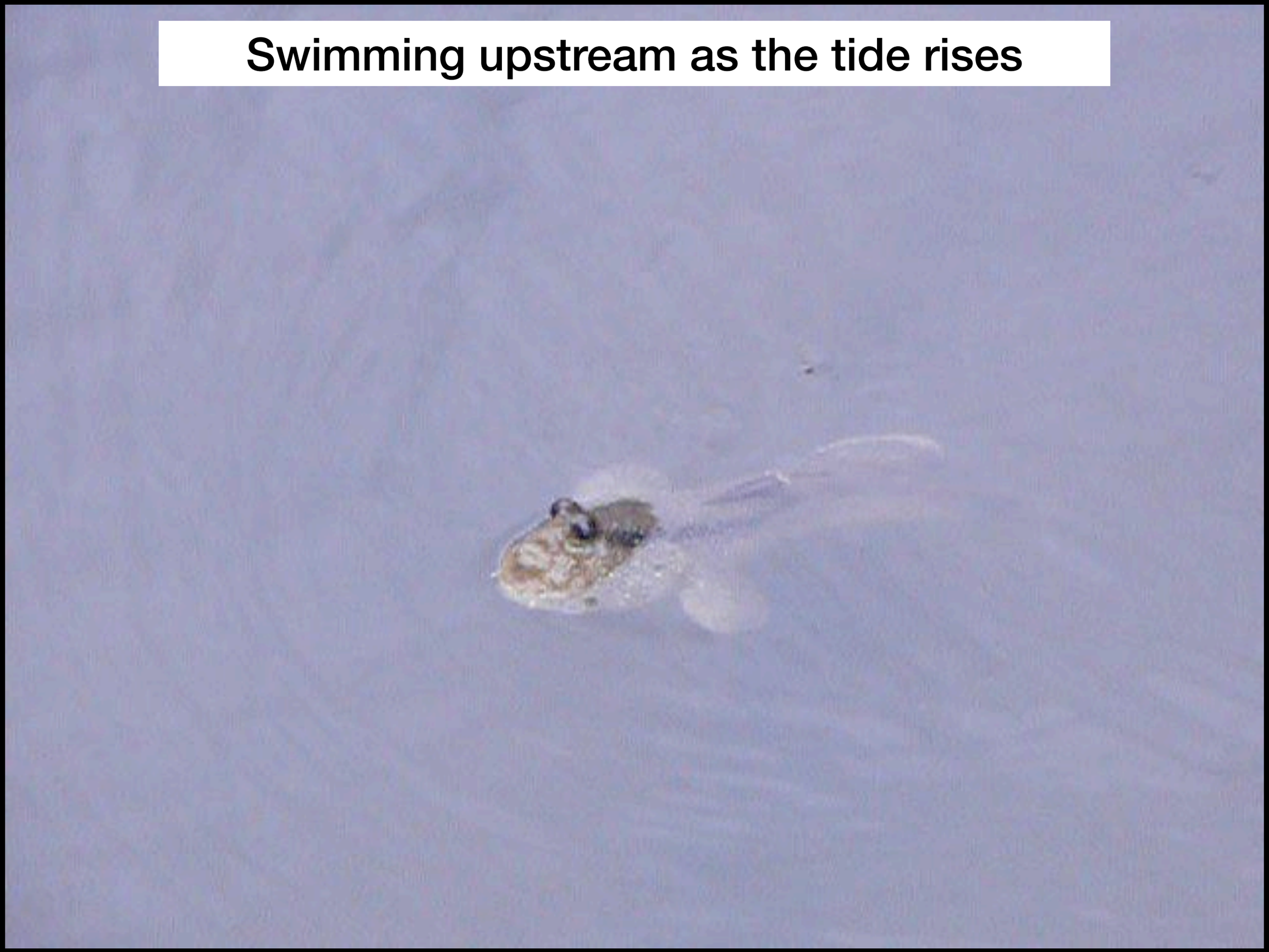
Tracks left behind by their ray-finned fins are a giveaway!

Mudskippers flee the high tide and may meet as they swim upstream. When too close, aggressive behaviour is expressed

Dorsal fin raising

Charge

Swimming upstream as the tide rises



Mudskippers seek refuge on tree trunks in the forest and are much closer to each other than when in their burrows (territorial compression)

4.2 Natal suppression and post-natal recovery of territory in smooth-coated otters

Tina Liow, 2019. Home range, activity pattern, and feeding ecology of pre-natal and post-natal smooth-coated otters (*Lutrogale perspicillata*) in Singapore. BSc Hons thesis (2018/19), Department of Biological Sciences, National University of Singapore.

Smooth-coated otters: the Central Watershed territory

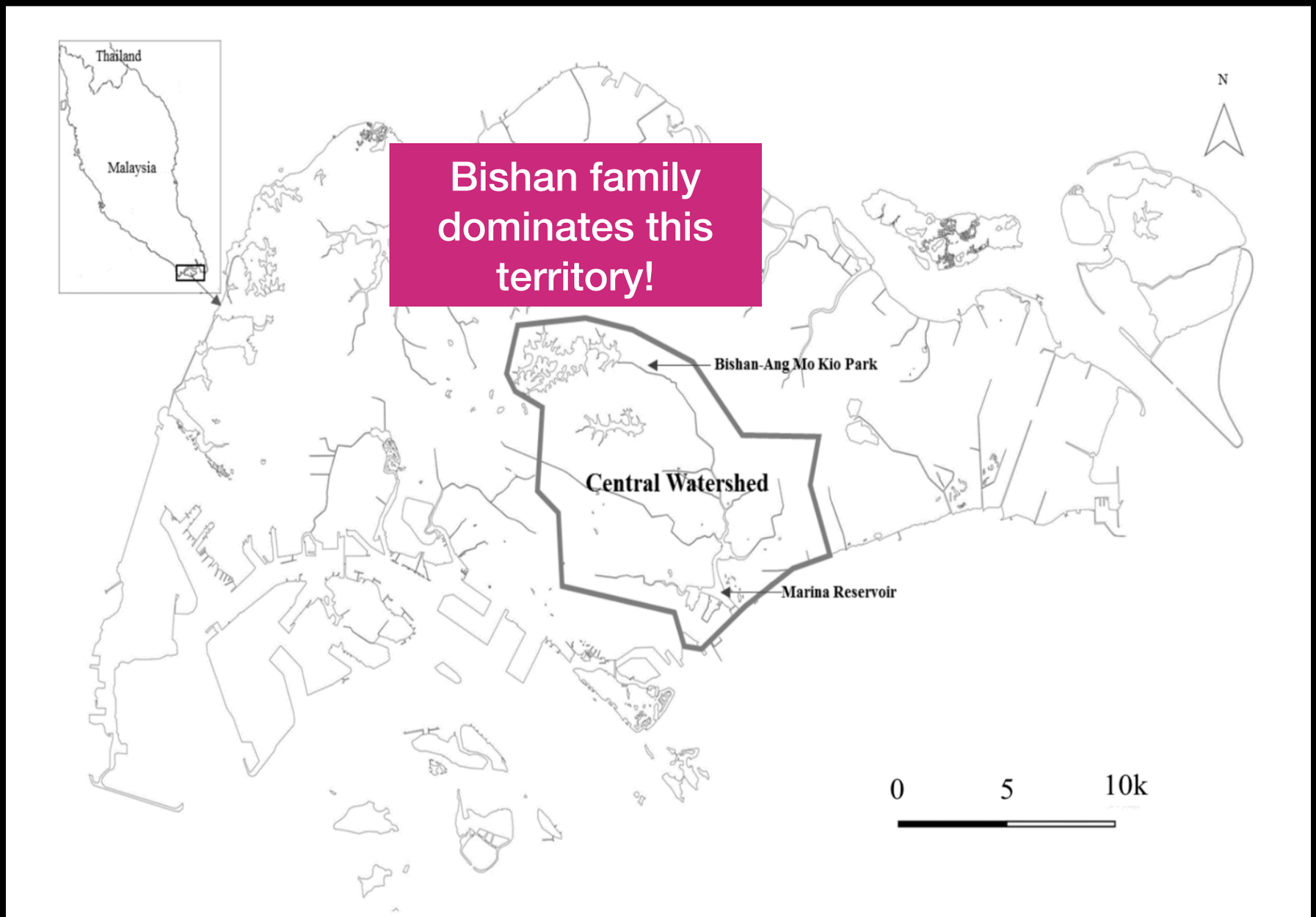


Figure 1. Map of Singapore showing the Central Watershed and the two areas where the two *L. perspicillata* groups established.

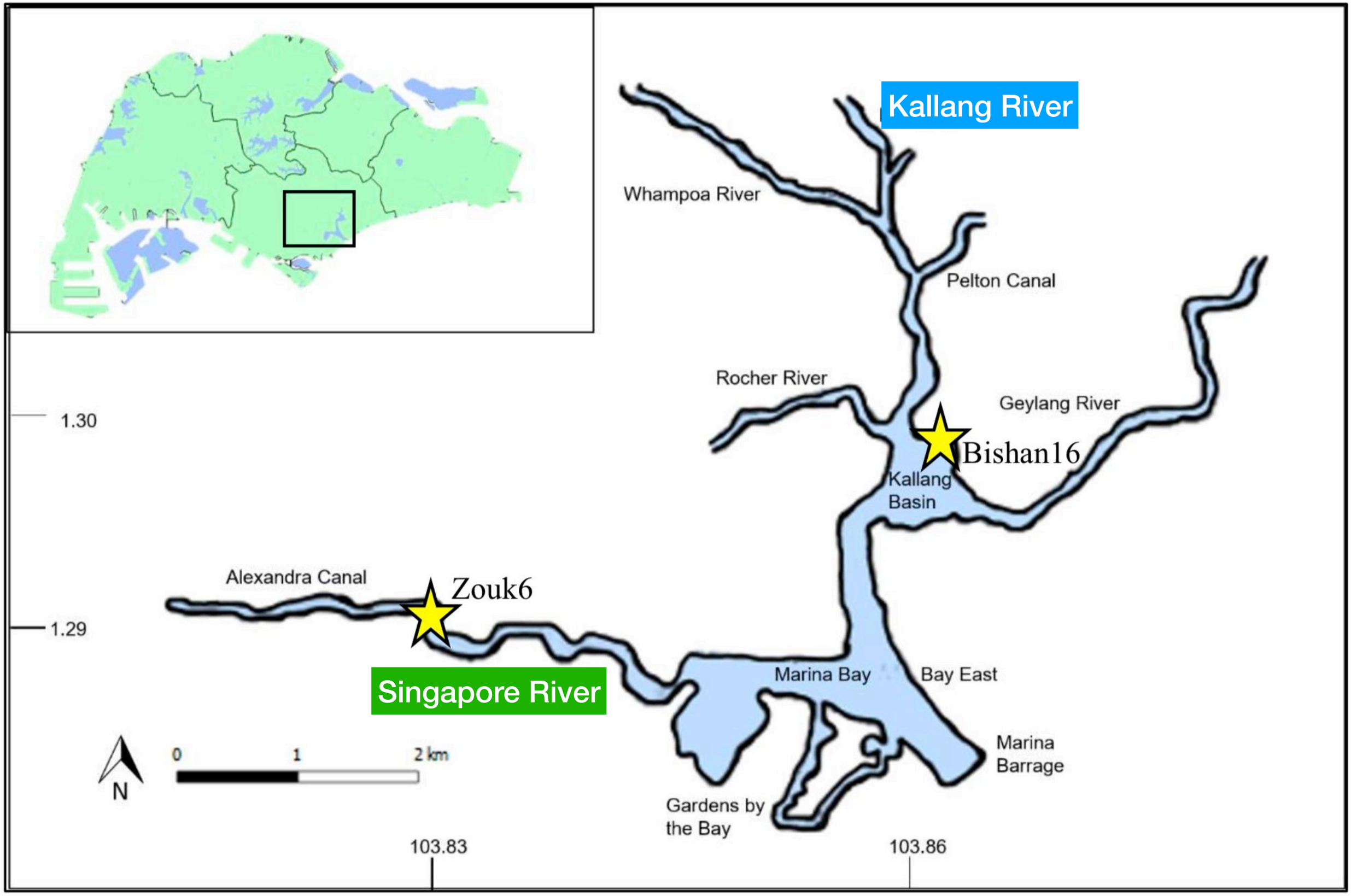
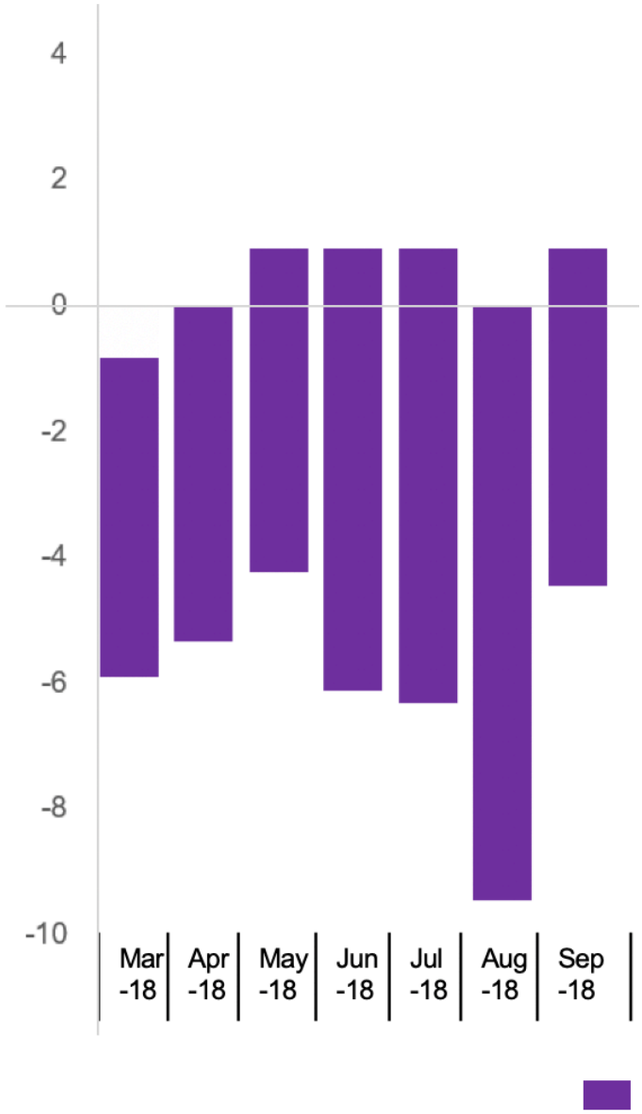
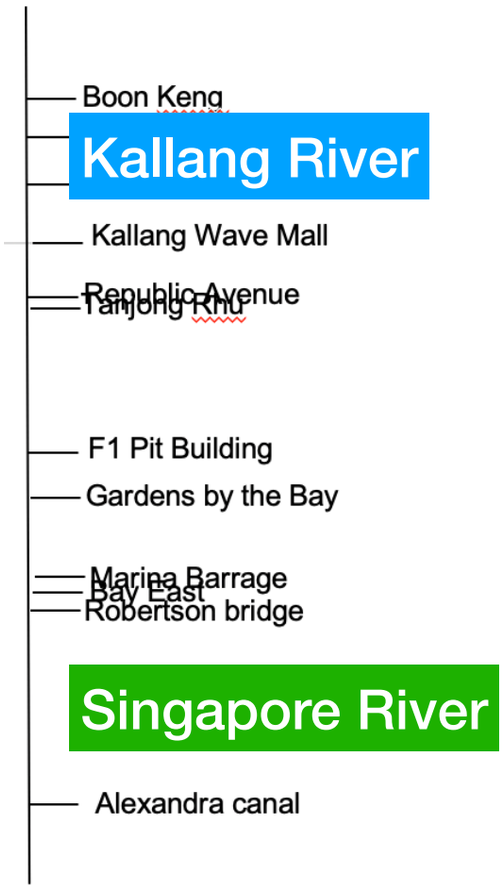


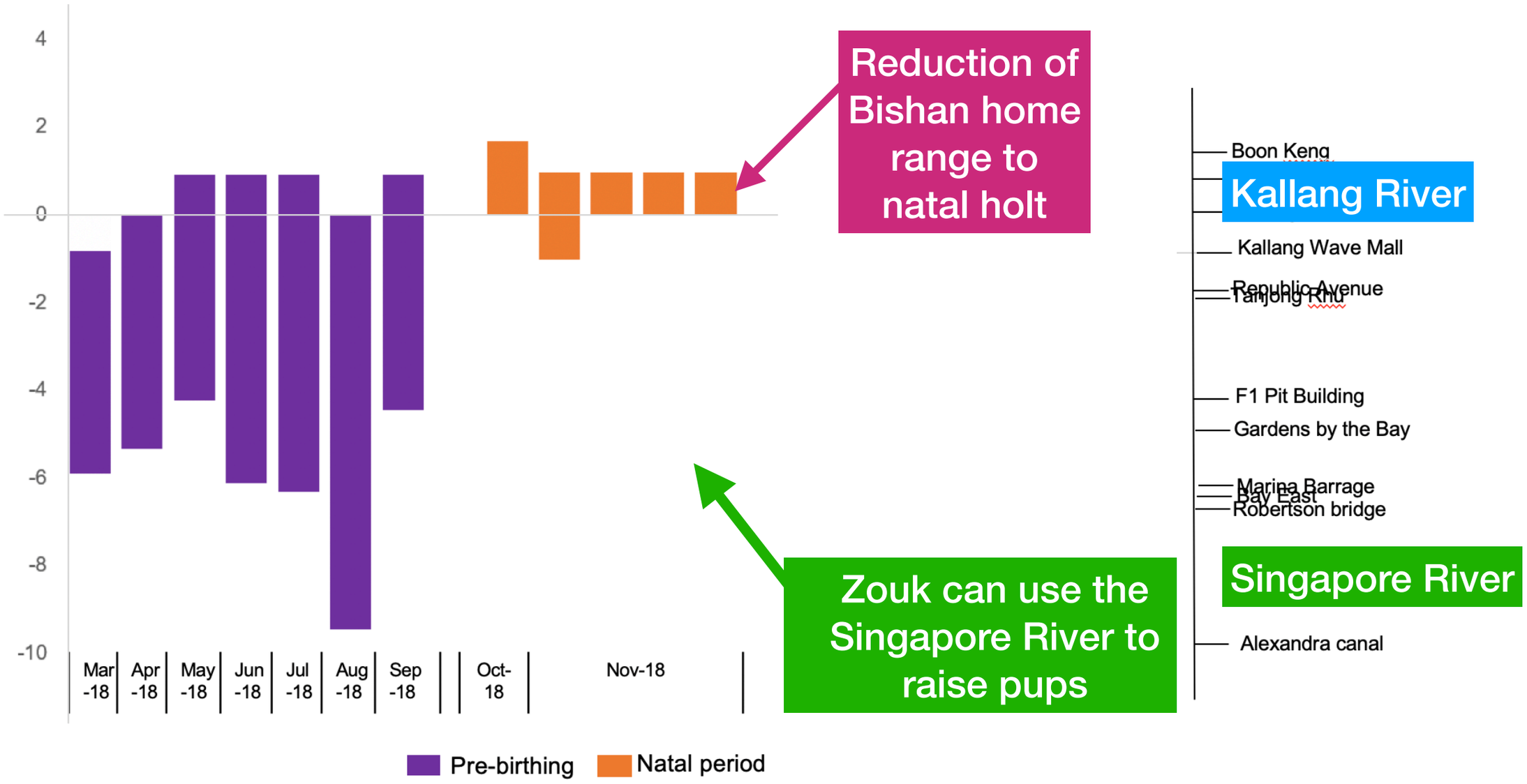
Figure 2.1. Map of Marina catchment, Singapore, denotating natal holt of Bishan16 and Zouk6. (Adapted from: OneMap)

Natal suppression and post-natal recovery of territory in Bishan family smooth-coated otters

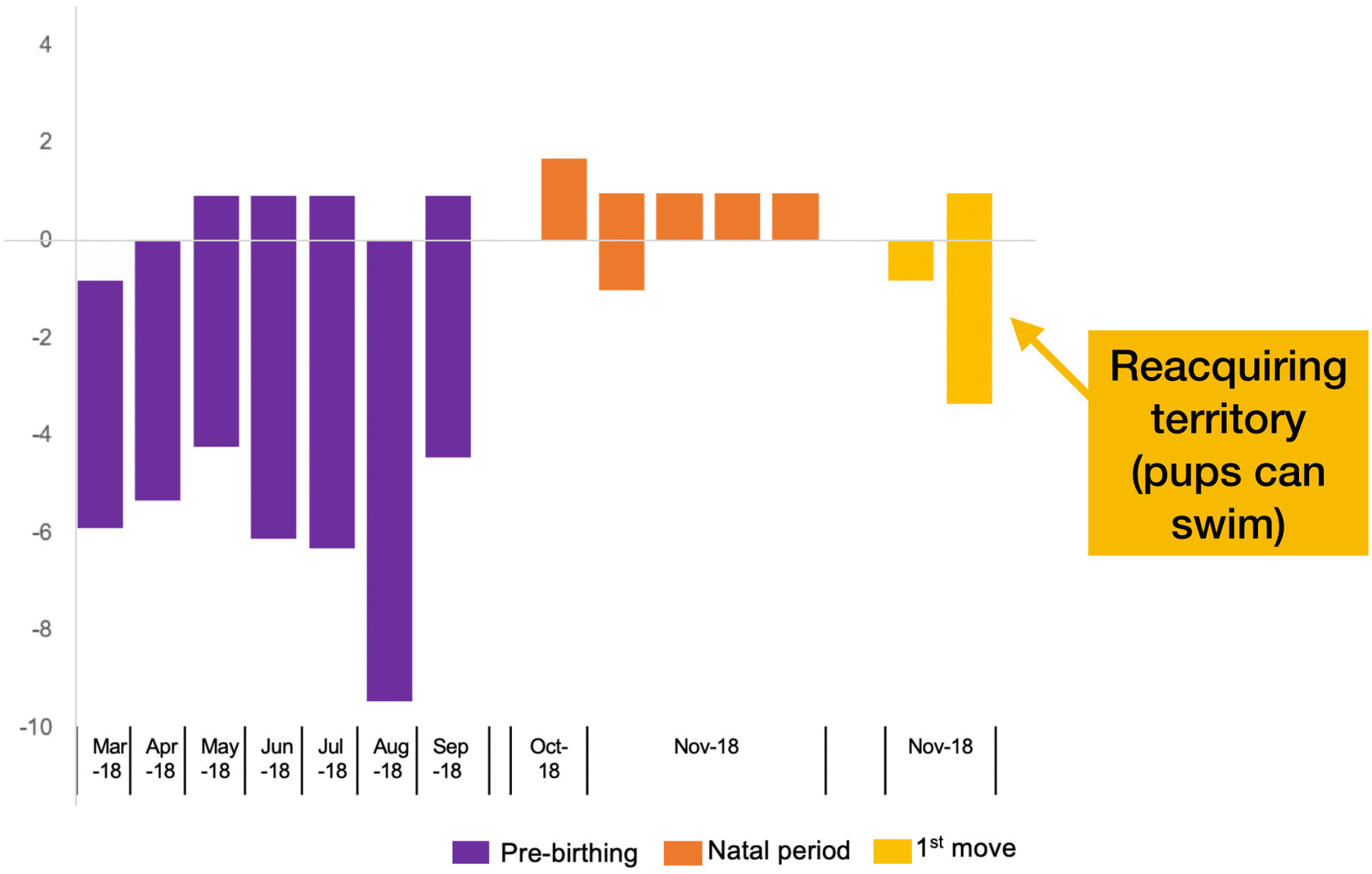




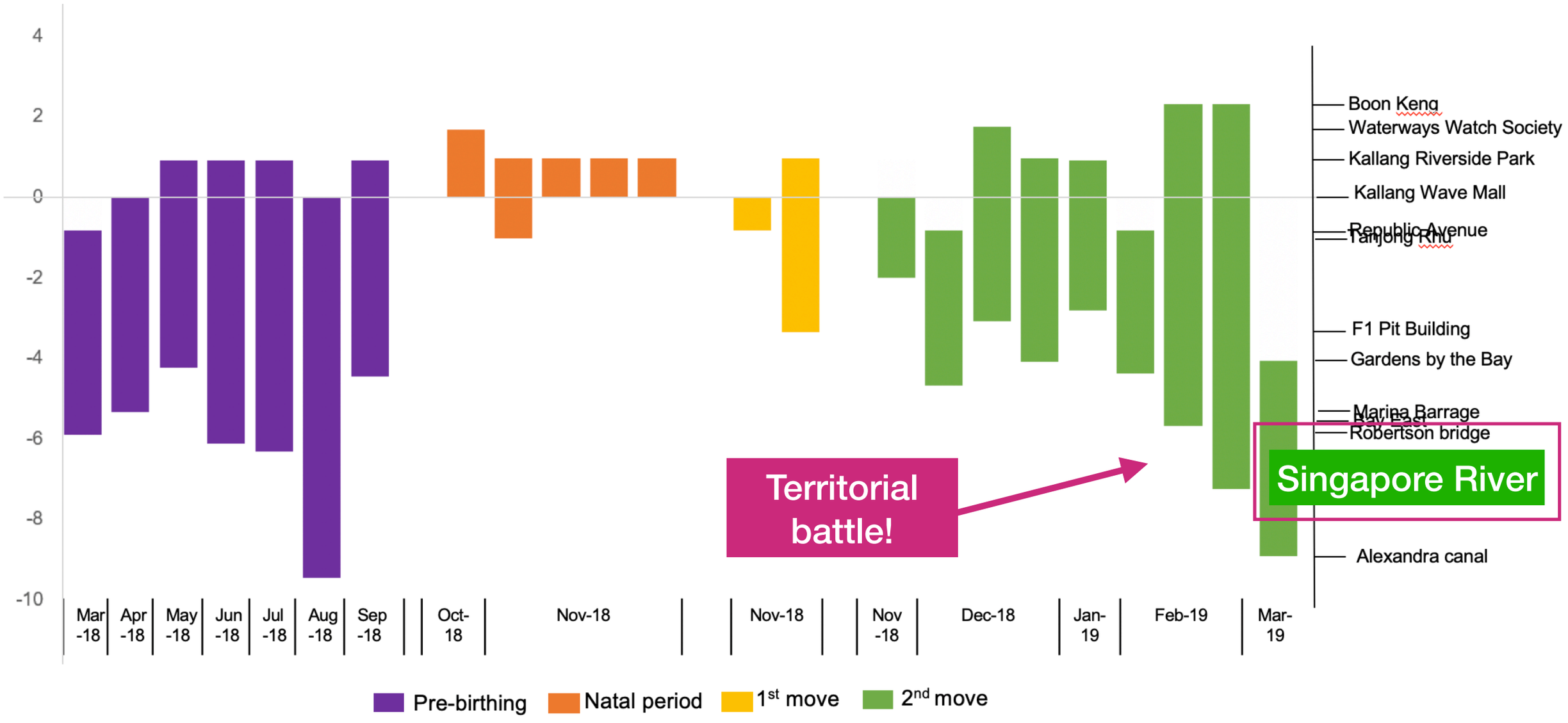
Natal suppression and post-natal recovery of territory in Bishan family smooth-coated otters



Natal suppression and post-natal recovery of territory in Bishan family smooth-coated otters



Natal suppression and post-natal recovery of territory in Bishan family smooth-coated otters



Bishan family chases away the rival Zouk family at Singapore River

Marjorie Chong

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5. Why do territory holders always win?

- 5.1 Arbitrary rule hypothesis
- 5.2 Resource-holding potential asymmetry hypothesis
- 5.3 Payoff asymmetry hypothesis

5. Why do territory holders win?

Observations in nature:

- Most territory owners don't forfeit their territories in conflicts with intruders.

- Territorial defense does not often escalate to full-blown fighting.

Maynard Smith, J. & G. A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

Game-theory approach to animal conflicts

Maynard Smith, J. & G.A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

- Three major hypotheses (suggested explanations) on the means by which animals resolve disputes.

1. Arbitrary rule hypothesis - resident always wins
   (supply of resource is high, or costs of fights very high)
2. Resource-holding power asymmetry hypothesis - better conditioned fighter wins
   (resident likely to be in a better condition)
3. Payoff asymmetry hypothesis - the individual with the "greater amount to lose" wins
   (resident is often more invested)

Game-theory approach to animal conflicts

Maynard Smith, J. & G.A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

Evaluating animal contests

- Animal contests are divided into:
- Symmetrical contests - contestants are evenly matched, outcome depends on the contestant who is able or prepared to fight longer

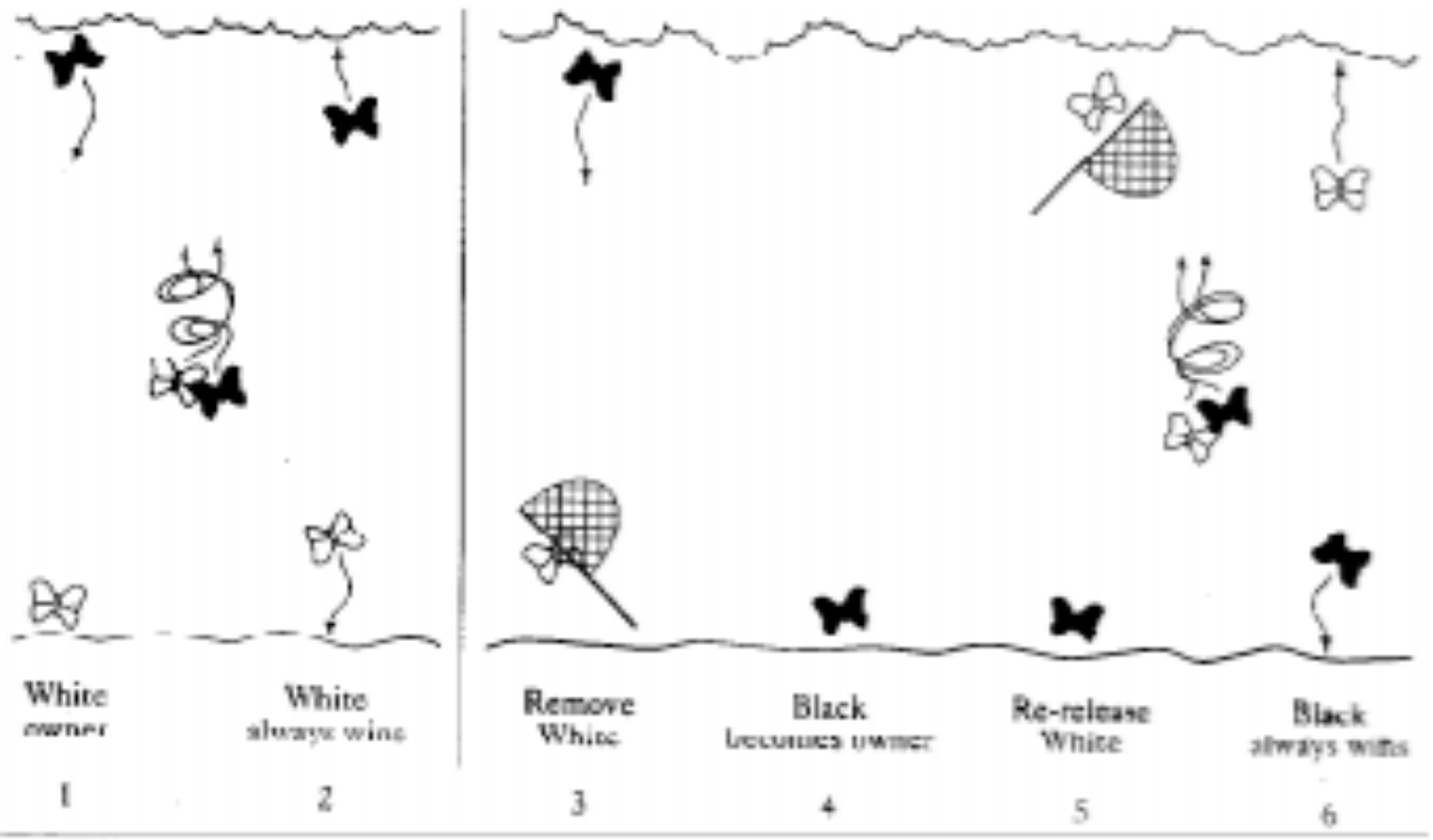
- Asymmetrical contests - outcome depends on the nature and strength of the asymmetry

5.1 Arbitrary-rule hypothesis

Resident always wins

(proposed in 1976)

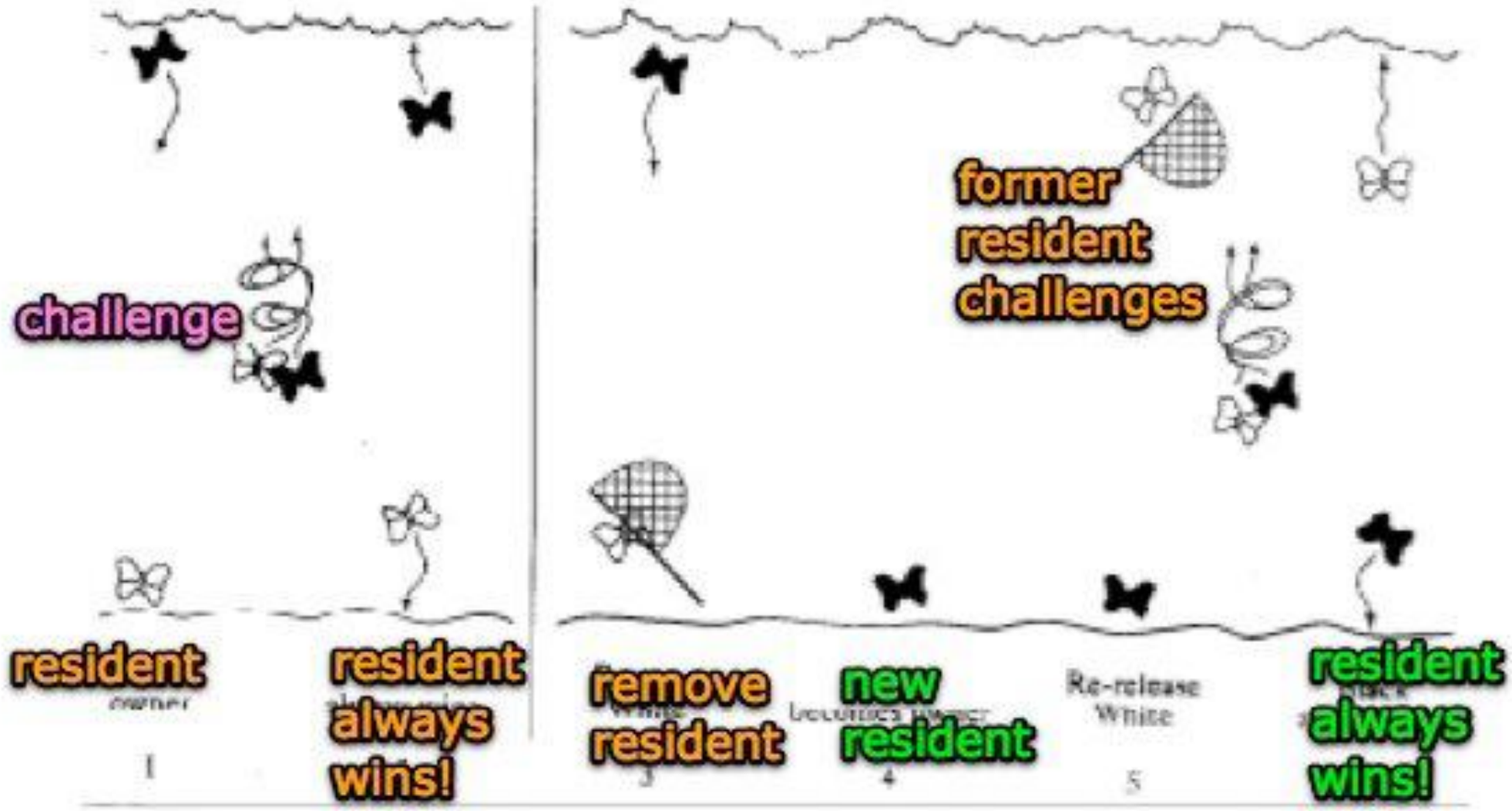
The arbitrary-rule hypothesis. Experimental evidence. (Taken from Alcock 1998)



Maynard Smith, J. & G. A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

5.1 Arbitrary-rule hypothesis
Resident always wins

The arbitrary-rule hypothesis. Experimental evidence. (Taken from Alcock 1998)



symmetric contests. Anim. Behav. 24: 159-175.

5.1 Arbitrary rule hypothesis – rejected!

Are animal contests settled by simple arbitrary rules, such as whoever holds territory wins?

- This explanation was rejected because the resource (sunspots) is plentiful
- Thus the attempts to acquire territories has no potential fitness payoff, and does not encouraging acquisition effort (not worth it)
- *Also removed residents were held in nets, so may been eager to escape than challenge*
- Hence, this experiment was later rejected as evidence for an explanation

5.2 Resource holding potential asymmetry hypothesis:

the larger and more motivated resident wins

- Individuals differ in their ability and motivation to fight (due to genetics, developmental history, age, physiology etc)
- The Resource Holding Potential of an individual is a measure of the absolute fighting ability of the individual (the motivation to continue when others give up). Note outcomes of challenges can be severe.
- "What benefit do I receive from this action"

Maynard Smith, J. & G.A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

5.2 Resource holding potential asymmetry hypothesis:
the larger and more motivated resident wins

Asymmetrical contest

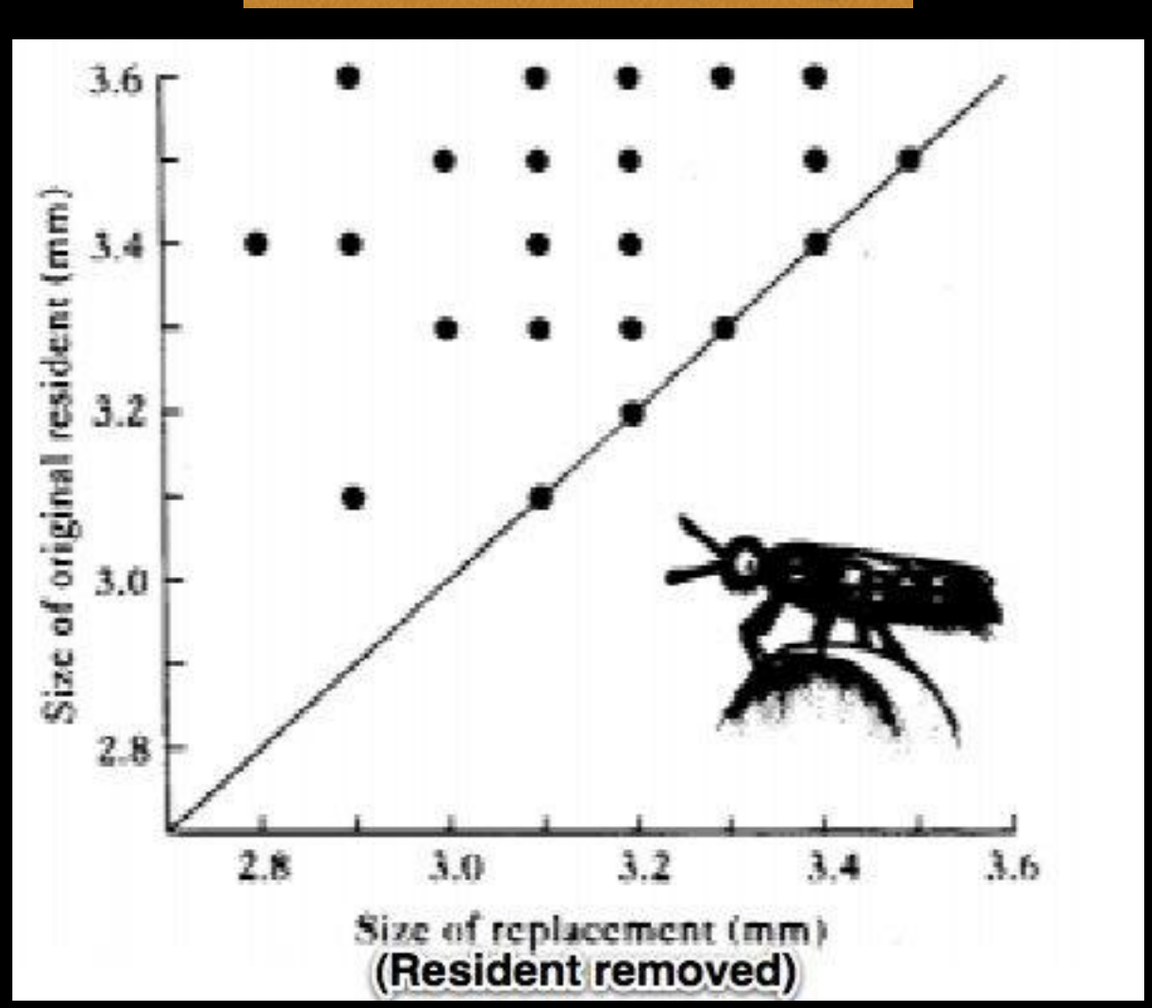
- Owners of a resource typically win challenges or are not challenged
- Why do challengers give up so easily? Residents are larger and more dominant (higher RHP).
- Is that how they became resident in the first place? Or was it a result of being resident?
- *"What benefit do I receive from this action"*

Maynard Smith, J. & G.A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

5.2 Resource holding potential asymmetry hypothesis:
the larger and more motivated resident wins

- Territory owners are bigger, stronger
  - E.g. studies with;
    - Beewolf wasps (right)
    - Pseudoscorpions
    - Damselflies

resident was always larger



5.2 Resource holding potential asymmetry hypothesis:
the larger and more motivated resident wins

- Residents are healthier due to having access to resources.
- They can fight for longer time and win a war of attrition.
- Cost to challengers may be too high to even attempt a challenge

5.3 Payoff asymmetry hypothesis
The (more to lose) resident wins

This is an asymmetrical contest because:

- While there are certain initial costs to acquisition of new territory,
- Payoffs increase over time because of "dear enemy" effect with familiar neighbours
- Who may even work on cooperative defense
- With benefits >> costs, the resident has much more to lose than any challenger!

Maynard Smith, J. & G.A. Parker, 1976. The logic of symmetric contests. Anim. Behav. 24: 159-175.

Tasmanian northern snow skink
by Nuytsia@Tas on Flickr

5.3 Payoff asymmetry hypothesis
The (more to lose) resident wins

- Male snow skinks in Tasmanian highlands
- Not strictly territorial; cross into each others home ranges: result = lots of male-male conflict just after hibernation, three months before mating season
- Body sizes were similar!
- Contests can escalate to torn limbs!

Olsson, M. & R. Shine, 2000. Ownership influences the outcome of male-male contests in the scincid lizard *Niveoscincus microlepidotus. Beh. Ecol*., **11**(6): 587-590.

Olsson and Shine • Male-male contests in scincid lizard

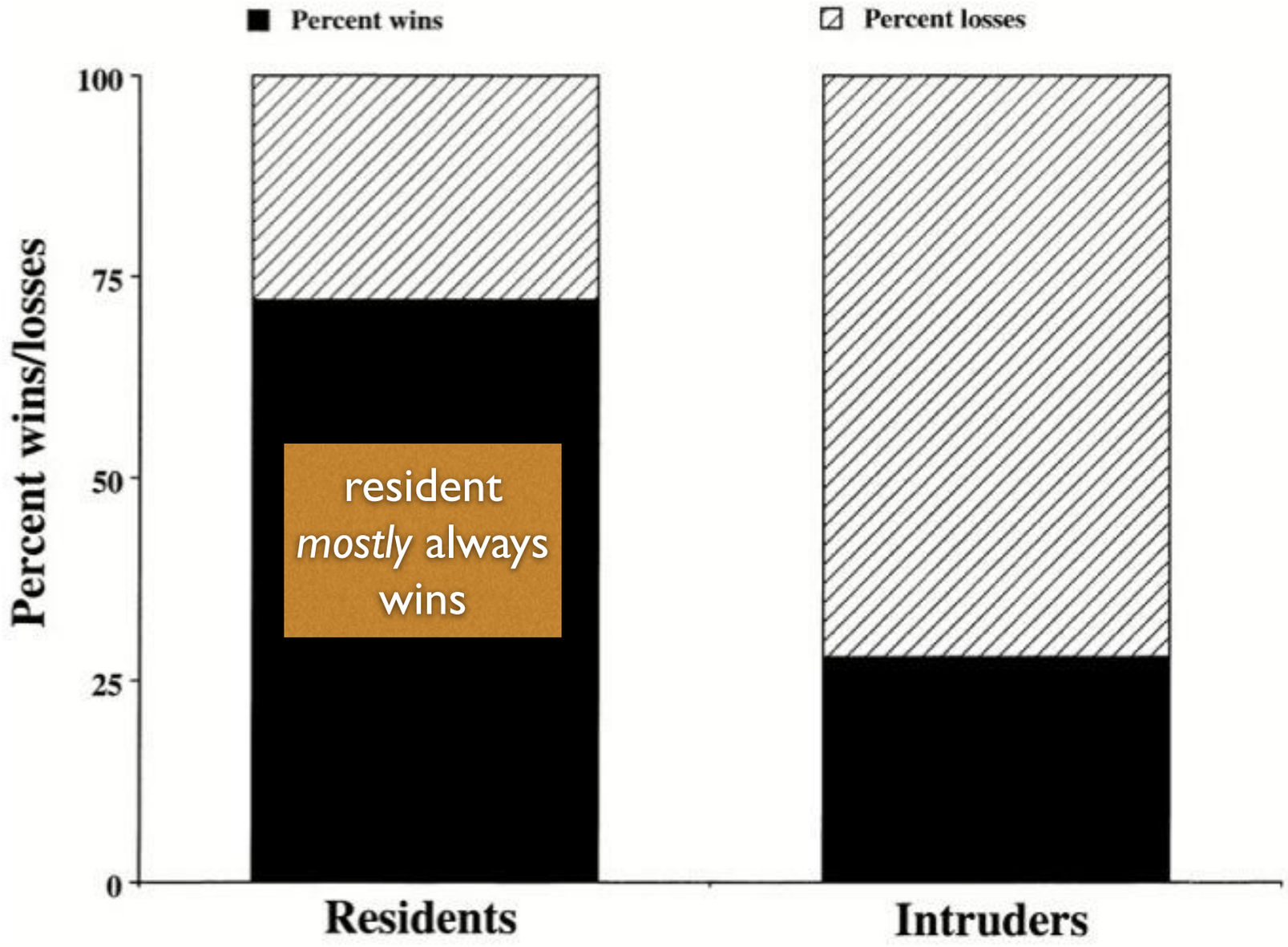


Figure 1
Effect of residency on the outcome of contests in male snow skinks.

Olsson, M. & R. Shine, 2000. Ownership influences the outcome of male-male contests in the scincid lizard *Niveoscincus microlepidotus. Beh. Ecol.*, **11**(6): 587-590.

5.3 Payoff asymmetry hypothesis

The (more to lose) resident wins

Resident males won 72% of bouts

- Male-male contest determined by residency
- It is a cold environment with a high population density
  - I.e. a home range with a sunspot (basking sites) is critically important to fitness

What about the 28% loss?

- The other male-male contest were determined by body size

Olsson, M. & R. Shine, 2000.

The winner was always *more motivated* or simply *much stronger*

LSM1303 Animal Behaviour
Lecture 7 Territoriality

6. Types of territories

- 6.1. Mating, nesting and feeding
- 6.2. Mating and nesting
- 6.3. Mating (lek)
- 6.4. Nesting
- 6.5. Feeding territory
- 6.6. Roosting
- 6.7. Winter territory
- 6.8. Deviates

1. Mating, nesting and feeding

- Most songbirds

2. Mating and nesting

- Food for young obtained elsewhere (foraging on neutral ground, indefensible, widely scattered)

Scarlet finch - aggressive but feeds communally away from the nest.

3. Mating (lek)

- Territory restricted to courtship and mating.
- e.g. Greater Prairie chicken
  - dawn courtship displays in central US, Canada; endangered
- inflation of colorful throat-sacs, foot-stamping, fanning tails, raising neck feathers, etc
- fights that may end in death!

4. Narrowly restricted nesting territory

- defend only immediate surrounding of nest (jab distance)
  - True of many colonial waterbirds
  - defend against pilferers of nesting materials
  - large colony deters predators

5. Feeding territories

- Often varies with food supply
- e. g. female tigers in Nepal (ave 8 sq. miles) vs Russian Far East (200 sq. miles)

- Unusual case: gull defends fishing boat against intruders; picknickers.

6. Winter territory

- not mating and nesting

- E.g. Kestrel, defends territory arounds nest, up to 10 sq. Km,
- In winter, readjusts, hunts in daylight hours during winter; up to 1 sq. km,
- depends on food availablity

7. Roosting territories

- Occupy same individual perches, e.g Starlings

A mixed flock of starlings, Daurian (Purple-backed) Starlings (*Sturnus sturninus*) and Asian Glossy Starlings (*Aplonis panayensis*)
[17 Oct 2010 by **NM Ong & Richard Lim]**

The starlings were roosting on the bare branches of a dead tree along Singapore's Serangoon Road (Bird Ecology Study Group)

8. Deviates/8.1 Sharing territory

Pied Wagtail

Sharing territory

- The Pied Wagtail defends riverside winter territories
- It forages on insects that wash up on banks
  - This is a renewable food source with every wash
  - Wagtails forage in a way which allows replenishment
- Intruders, are tolerated under certain circumstances

How do dominant pied wagtails share territory?

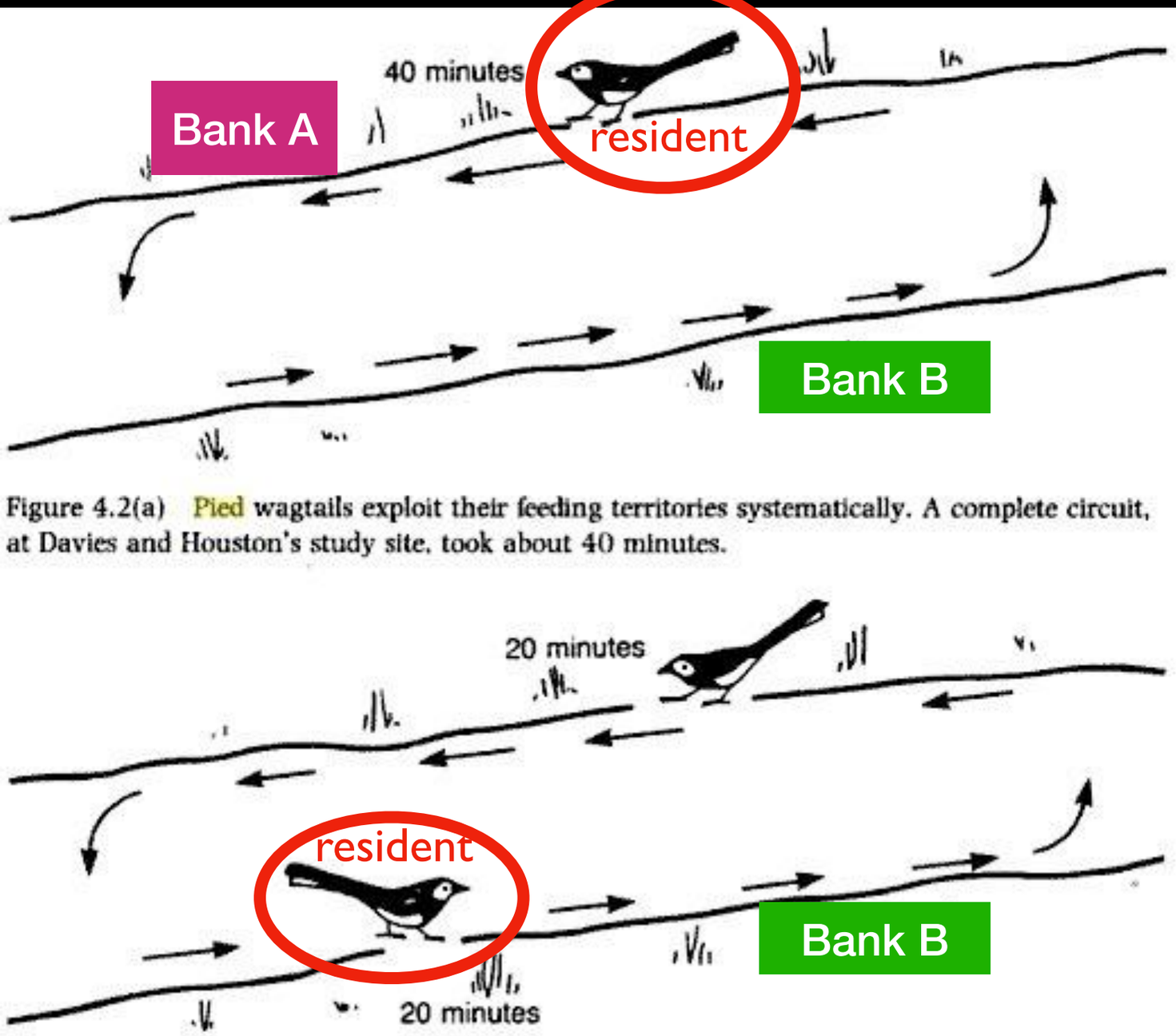


Figure 4.2(a) Pied wagtails exploit their feeding territories systematically. A complete circuit, at Davies and Houston's study site, took about 40 minutes.

Figure 4.2(b) When a territory is shared between two pied wagtails, each walks approximately half a circuit behind the other, and so crops only about 20 minutes' worth of new food.

1. Resident wagtail harvests insects on Bank A

2 Resident moves to Bank B

3. Resident tolerates intruder feeding on Bank A, which is partially harvested

4. When river replenishes the bank, the resident gets the first pick of food on Bank A

5. Other birds in the vicinity (competition) are kept out of this area by the two birds, most of the time.

Sharing territory

- Sharing: profitability of foraging site decreases, territorial defense increases
- Owners know which area has been cropped; intruders do not
- Satellite defense contribution up to 20-54% of territory
- Satellites tolerated only when food availability is high

8. Deviates/8.2 Bypassing territories: Sneakers and satellites

- Bluegill sunfish (*Lepomis macrochirus*)
- Fish reproduction
  - Males build nests; attract females, protect nest
- External fertilisation, i.e. egg and sperm released into water,
- synchronised sexual behaviour mediated by pheromones

Bluegill Sunfish (Lepomis macrochirus)

Photo by Mark Grapengater

Neff, B. D., P. Fu & M. R. Gross, 2003. Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behav. Ecol.,* 14(5): 634-641.

Parentals, sneakers and satellites

Three types of males/tactics:

1. **Parental** - older, territorial males
   (mature later, wait; bourgeois)
   (>= 7 years old)

2. **Sneaker** - younger, dart in and shed sperm
   (precocious, steal; parasitic)
   (2 - 4 years old)

3. **Satellite** - intermediate age, mimic females,
   enter territory slowly, shed sperm
   (precocious, steal; parasitic)
   (4 - 6 years old)

Parentals, sneakers and satellites

Comparing sperm longevity and density

Long-lasting, low density!

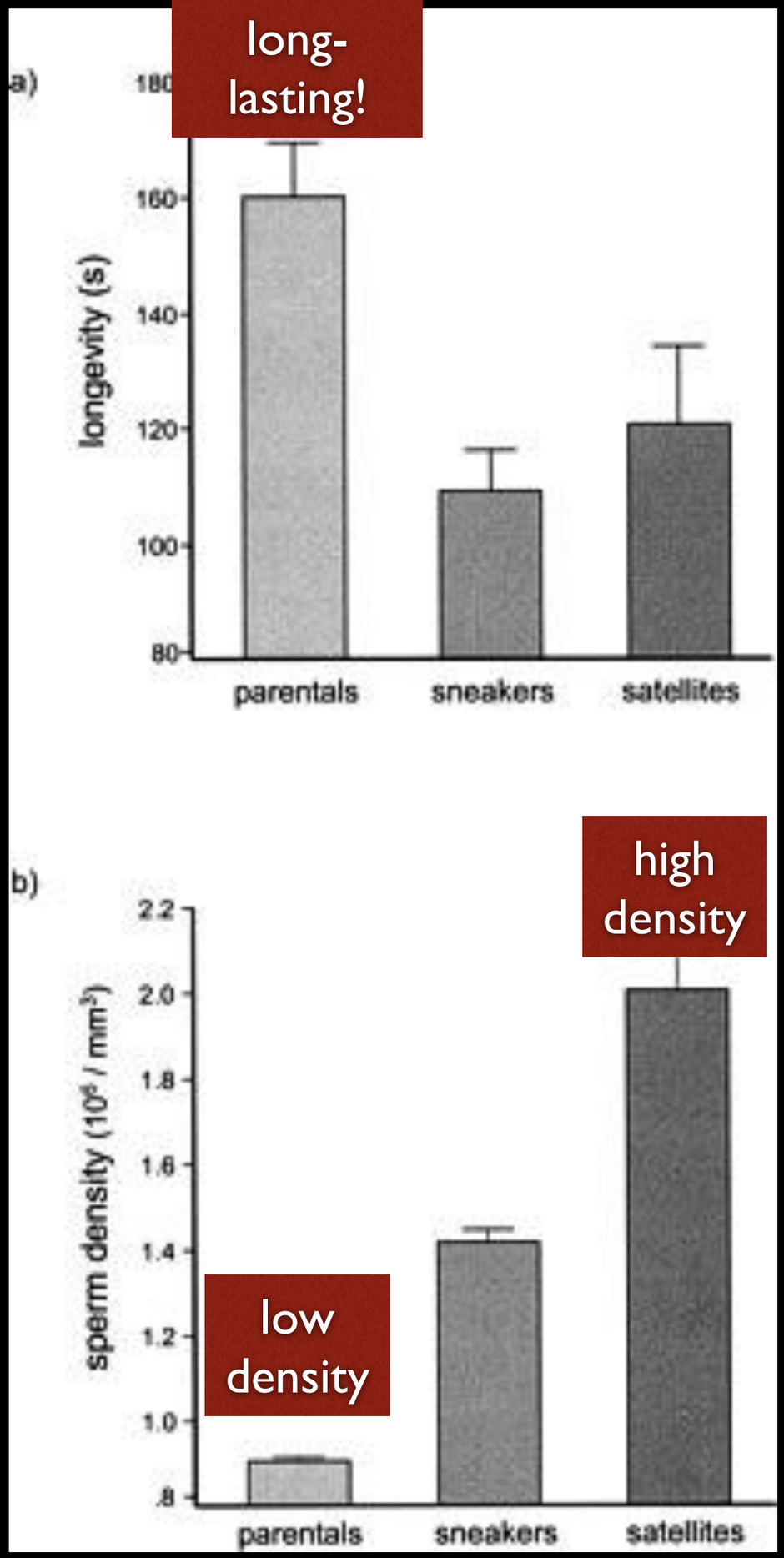
Parentals have low density sperm, but it lasts a long time

high density

Satellites have the highest density and half the longevity

Medium longevity and density

Sneakers range in between



Parentals, sneakers and satellites

	Parentals	Satellites	Sneakers
Rel. testes size	smallest	intermediate	largest
Sperm life	longer	shorter	shortest
Sperm density	lowest	greatest	intermediate
Sperm swim speed and energy	slower; less	intermediate	faster; greater

Life history choices

- Resources invested towards reproduction
  - Smaller individuals deliver sperm, younger age (always experiences sperm competition but highly competitive: 89%/67% success in direct competition
- Resources invested towards growth
  - Larger males secure territory, attract females invest in mate/nest guarding (exclude sneaks), reduce sperm competition (10-20%)

Life history choices

Why do all three strategies exist?

Think of cost versus benefit.