National University of Singapore

LSM1303 Animal Behaviour

Lecture 6: Foraging

N. Sivasothi aka Otterman

What have we learnt so far?

- Wildlife in Singapore
- Diversity, ethology and ethics
- Innate behaviour and Learing
- Living in Groups
  also communication, courtship, foraging and the fact benefits must outweigh costs in various strategies

Preamble: Foraging

- An important activity for survival (hence common observed)
- Requires energy, i.e. expand energy to acquire food
- Many steps involved
- Different types: solitary and group – benefits must outweigh costs
- Much of foraging involves learning

Case study – points to note from the BBC "learning by trial" video

- Prey selection – younger individuals are less strong or experienced, so easier to target, but must isolate from healthy, heavy mother
- Reduce distance (approach) – flatten body amidst the long grass, stay camouflaged as long as possible
- Ambush strategy – cheetah's burst of speed while prey is unaware
- Group hunting – Zebras are large but three cheetahs may be able to take on a large-sized prey
- Coordination – experienced hunters will replace each other at point position to persistently tire out a single target

Cheetah trio hunt Zebra: learning by trial (BBC)

Case study – points to note from the spotted hyaena hunting video

- Prey selection – younger individuals are less strong or experienced, so easier to target, but must isolate from healthy, heavy mother
- They focus on group on a single prey
- Group hunting – larger mother is kept at bay by some hyaena
- Coordination – this is an experienced group
- They have to defend their kill
- Predators provide for other animal in the ecosystem

Spotted hyaenas hunting larger prey

Foraging

1. Objective of feeding
2. Foraging is a series of discrete decisions
3. Diet choice and strategies
4. Food handling
5. Optimal Patch Choice
6. Optimal Prey Choice
7. Avoiding predation

Optimal foraging theory

Breed & Moore 2011: Chapter 9 Foraging

CHAPTER 9

Foraging

CHAPTER OUTLINE

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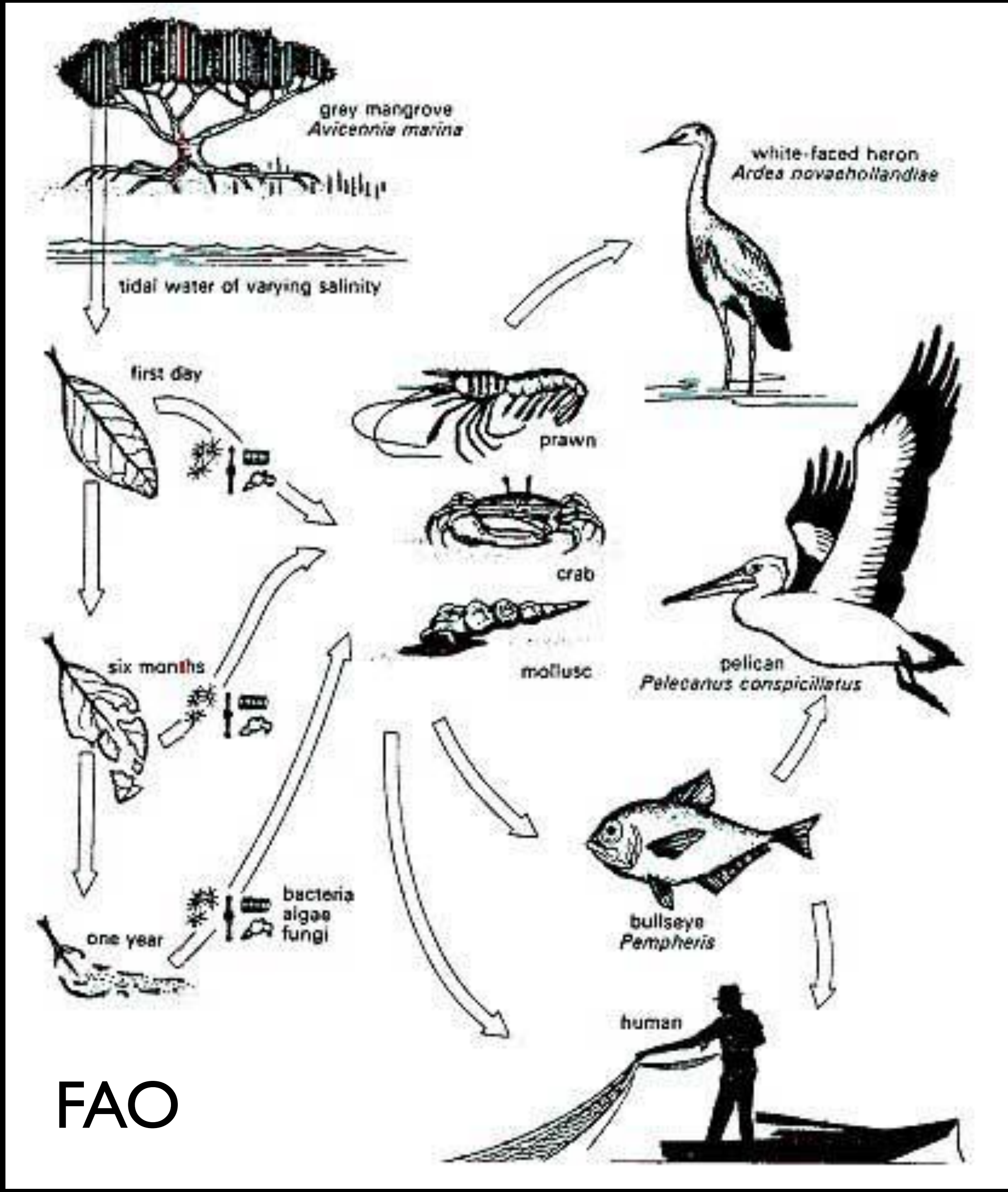
1. The need to feed

The need to eat

- Energy from the sun
- Photosynthesised by plants
- Animals have to eat plants or other animals to obtain energy



Why feed?

- An adequate diet
  - gain enough energy to support growth, development, and reproduction
  - *gain the right nutrients*
- E. g. Sodium limited herbivores inland
  - Sweat bees
  - Puddling by butterflies
  - Salt licks visited by mammalian herbivores (geophagy)
- Indigestible cellulose!
  - microbial symbiosis
  - fermentation chamber
- Cats and dogs
  - chewing vegetation

rainycity@flickr

Sweat bees

'Sweat bees' drinking up!

Butterfly puddling, Fraser's Hill (26 Jul 2017)

Butterfly puddling, Fraser's Hill (26 Jul 2017)

Butterfly puddling

- When a butterfly's proboscis is unfurled and probing the ground for water and nutrients at water puddles, mud, dung or carrion
- The butterfly sips water rich in mineral salts and other essential nutrients that have leached from the surrounding soil and rocks.
- Male butterflies do more puddling than females.

https://butterflycircle.blogspot.com/2008/11/why-do-butterflies-puddle.html

Butterfly puddling

- A few seconds to more than an hour (intoxicating)
- A nectarivore diet lacks sodium, which (along with other minerals) is required for various functions, including flight and pheromones
- Mostly younger males puddle; they are more active - need to locate receptive females
- Nuptial gift to each female includes minerals, amino acids

Butterfly puddling

The butterfly is resting on the ground, with its proboscis inserted into ‘puddle’ of a nutrient source on the ground

https://butterflycircle.blogspot.com

Butterfly puddling

When a butterfly consumes high amounts of fluids containing a desired nutrient, it will excrete large amounts of water

Liquid spray releases excess fluids

https://butterflycircle.blogspot.com

Butterfly puddling

Sodium or Nitrogen?

- Study at Mt Kinabalu (1999): baited 227 individuals (46 species) at a rainforest site, 534 individuals (54 species) a farmland site
  - Water limited? No - many eject surplus water
  - Some are sodium limited - visually detect others to locate resource (attracted to decoys)
  - Some are protein limited - use smell to detect nitrogenous resource (decaying organics)

Beck, J., E. MuÈhlenberg & K. Fiedler, 1999. Mud-puddling behavior in tropical butterflies: in search of proteins or minerals? *Oecologia*, 119(1): 140-148.

Butterfly puddling

Sodium or Nitrogen?

- Study in Kuala Belalong, Brunei (2007):
- "Species that do react to amino acids tend to be among the most long-lived taxa in the community, suggesting that amino acids are a key variable to attain long life spans."

Beck, J., 2007. The importance of amino acids in the adult diet of male tropical rainforest butterflies. *Oecologia*, 151(4): 741-747.

Puddling congregation -
jostling for the best spots

<u>Similarly, for mammals</u>

herbivores in particular, consume soil (geophagy) or water from mineral-rich 'salt licks'

In addition to dietary supplements, other reasons have been suggested including to dealing with dietary toxins, diarrhoea, endoparasites or to adjust gut pH.

Kreulen, D. A. (1985). Lick use by large herbivores: a review of benefits and banes of soil consumption. Mammalian. Rev. 15, 107–123.

<u>Mammals at salt licks:</u>
orang utan in tropics

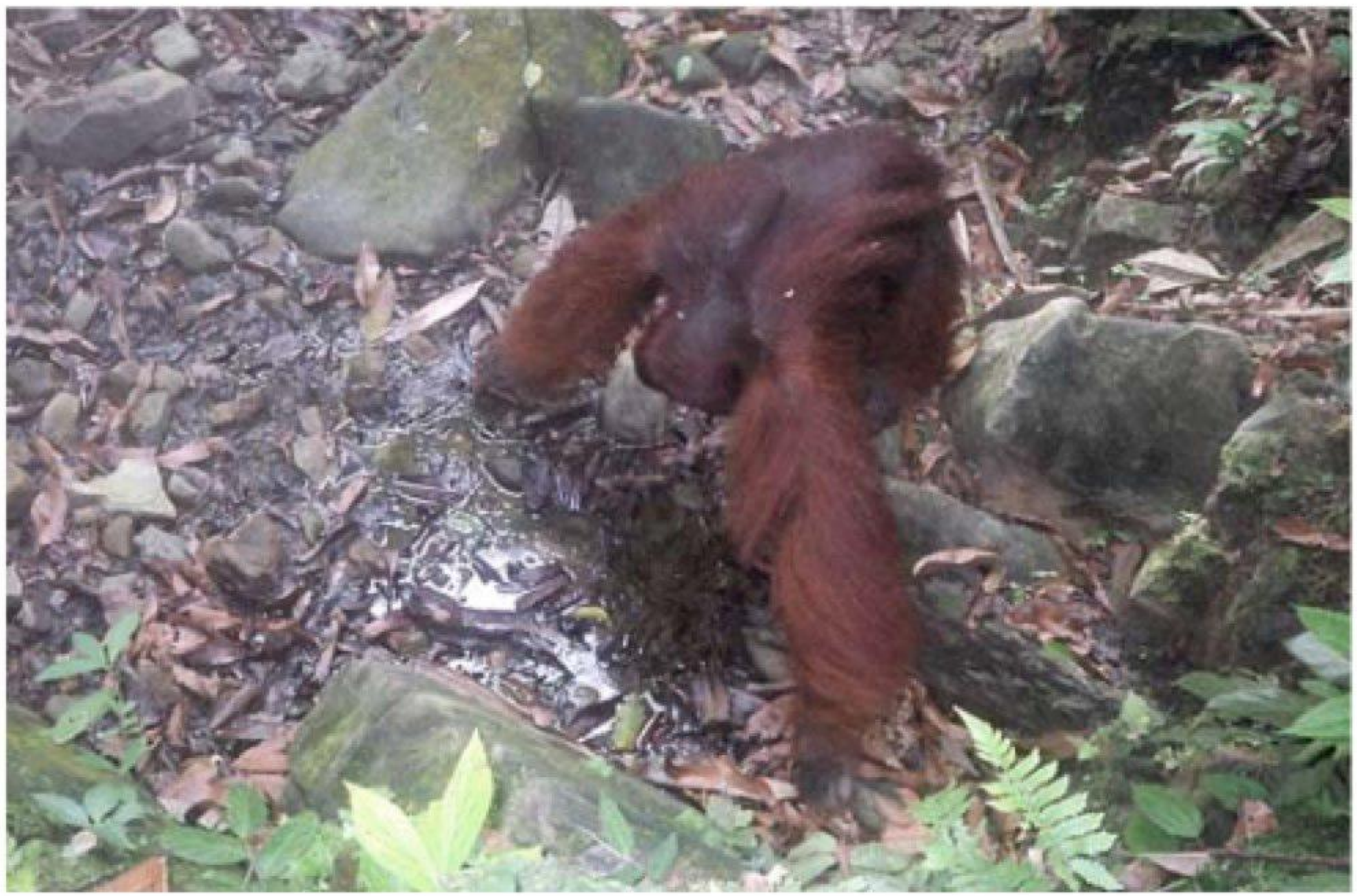


Fig. 4 Camera trapped adult-male orangutan at a natural lick in Deramakot forest reserve

Matsubayashi, H., Lagan, P., Majalap, N., Tangah, J., Sukor, J. R. A., & Kitayama, K. (2007). Importance of natural licks for the mammals in Bornean inland tropical rain forests. Ecological Research, 22(5), 742-748.

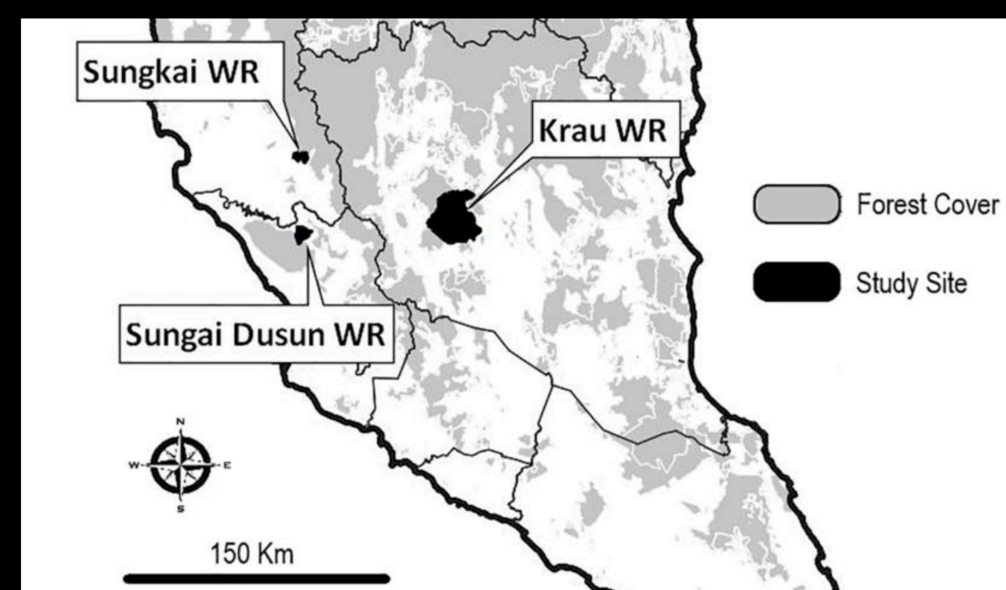
Mammals at salt licks

Geophagy by spider monkeys in neotropics

(BBC; via Arkive)

Common name	Scientific name
Species recorded at artificial saltlick and forest sites	
Wild pig	*Sus scrofa*
Malayan tapir	*Tapirus indicus*
Mousedeer spp.	*Tragulus* spp.
Southern red muntjac	*Muntiacus muntjac*
Malayan porcupine	*Hystrix brachyura*
Pig-tailed macaque	*Macaca nemestrina*
Sambar deer	*Rusa unicolor*
Short-tailed mongoose	*Herpestes brachyurus*
Malay civet	*Viverra tangalunga*
Long-tailed porcupine	*Trichys fasciculata*
Squirrels	–
Rats/mice	–
Banded civet	*Hemigalus derbyanus*
Species recorded only at artificial saltlick sites	
White-thighed langur	*Presbytis siamensis*
Long-tailed macaque	*Macaca fascicularis*
Sun bear	*Helarctos malayanus*
Common palm civet	*Paradoxurus hermaphroditus*
Large Indian civet	*Viverra zibetha*
Masked palm civet	*Paguma larvata*
Small-clawed otter	*Aonyx cinerea*
Marbled cat	*Pardofelis marmorata*
Golden cat	*Catopuma temminckii*
Leopard	*Panthera pardus*

Mammal species that turned up at artificial salt licks in Malaysia.



Simpson, B. K., Nasaruddin, N., Traeholt, C., & Nor, S. M. (2020). Mammal Diversity at Artificial Saltlicks in Malaysia: A Targeted Use. Frontiers in Environmental Science.

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2. Foraging is a series of discrete decisions

Foraging is a series of discrete decisions

- Foraging is the process of food-collection
- Foraging IS NOT a single decision,
- but a series of discrete decisions:
    - i) search; ii) locate (incl. stalk),
      iii) acquire (pursuit, subdue/kill);
      iv) handle, v) process and vi) consume

The complexity of decision-making by predators:
How does a cheetah hunt?

- The choice to hunt (acquire) involves decisions:
  - Choosing prey
  - Environmental conditions
  - Predators / competitors in the area (always vigilant)
  - Influence of presence of young

Mike Richardson and Sarah Winch, May 2011

When does a cheetah hunt?

Factor	Effect
Presence of preferred prey (various herbivores)	+ve
Presence of competitors (lions , hyaenas)	-ve
Energy needs (cubs, hunger)	+ve
Cover availability	+ve
Daylight	+ve

Cooper, A. B., Pettorelli, N., & Durant, S. M. (2007). Large carnivore menus: factors affecting hunting decisions by cheetahs in the Serengeti. *Animal Behaviour*, 73(4), 651-659.

‘various herbivores’

Size, health and alertness of prey matters too

Grant’s Gazelle
(*Nanger granti*)
[Stig Nygaard, 2010]

Thomson's gazelle
(*Eudorcas thomsonii*)
[Yathin S Krishnappa, 2009]

Black wildebeest,
Connochaetes gnou
[Derek *Keats*, 2016]

Video 1 of 3 – Cheetah hunting: Vigilance, search, choice (BBC)

Toto's mum hunting

- Spots a vulnerable gazelle
- Identifies opportunity; scans for competitors or predators
- Exerts more effort than normal (easy prey)
- Vulnerable gazelle mum has to abandon young to protect itself

Cheetah and Thomson Gazelle: Vigilance, search, choice (BBC)

Video 2: Cheetah hunting Thomson's gazelle: pups learn by observation (BBC)

<u>Honey hunting, observed by her three pups</u>

- Note the posture of hunting cheetah
- Pups stay behind, cued by the mum's behaviour
- Honey's selection of prey: focus on prey is directed at a specific individual
- Scientist's admiration for a highly efficient hunting ability; this can vary among individuals; with age and aptitude

Cheetah hunting Thomson's gazelle: learning by observation (BBC)

Video 3: Cheetah hunting wildebeest: technique and vigilance (BBC)

Honey and her three pups

- Pups had stayed hidden
- After the disturbance of a hunt, mum scans surrounding, determines its safe for pups to emerge
- Camouflaged pups emerge in response to a specific contact call by the mum

Cheetah hunting wildebeest: technique and vigilance (BBC)

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3. Diet choice and feeding strategies

3. Diet choice and feeding strategies

- Foraging behaviour depends on the dietary choice
- Consider these feeding habits…

i. Filter or Suspension feeders

ii. Predator satiation

herbivory

iii. Browsers and grazers

iv. Folivory

v. Frugivory

carnivory

vi. Pursuit

vii. Stealth

viii. Stalk and rush

ix. omnivory

Diet choices and influence on behaviour

i) <u>Filter or Suspension feeders</u>

- Food comes to it!
- Hence immobile

Sea anemone
[Arthur Anker, Bali, 2012]

Diet choices and influence on behaviour

ii) <u>Predator satiation</u>

- Produce many defenceless offspring
- This vulnerable stage is rare, not frequent
- More than predator can consume
- Thus some survive

Fig 1. High density of emergence of periodical cicadas. Taken by Dr. John Cooley.

Dr. John Cooley, Univ. Maryland Dept. Entomology

Diet choices and influence on behaviour

herbivory

- iii) Browsers and grazers
  - browsers (above ground; leaves, bark, stems; too high?)
  - grazers (on ground; affected in seasonal climes by snow)
- iv) Folivory - leaves, stems of plant.
  - Animal tends to be less active than fruit or meat eaters as the digestion process is longer
    - bigger digestion chambers (cellulose digestion),
    - longer intestinal tract (extract breakdown product)
- v) Frugivory - fruit eaters
  - More active species; compared to grazers
  - Has a shorter gut as extraction of fruit sugars is easier

Plants have defences!

Diet choices and influence on behaviour

carnivory

Carnivory (& Insectivory)

- vi) <u>Pursuit</u> – speed of the cheetah; plummeting fish; insect-eating birds, dragonfly or insect/fish-hunting spiders
  - Track by steering
  - Interception (aim for front of flight path)
  - Hunting in groups (Lecture 4 Cooperative Hunting)

Gary Eyring, 2008

Diet choices and influence on behaviour

carnivory

Carnivory (& Insectivory)

- vii) Stealth
  - Full-out pursuit by a heavy animal is tiring, but weight helps to overcomes prey
- viii) Stalk and rush
  - Surprise is distance-reducing
  - Good cover critical
  - Camouflage: colouration and behaviour

Emarone, 2009

Fishing spider hunting: identify the steps

The Singapore Fishing Spider (*Thalassius albocinctus*)

A Guide to Common Singapore Spiders

by Joseph K H Koh

Singapore Fishing Spider

Thalassius sp. (Doleschall) 1859

Can attack fish by diving into water and dragging it ashore for feeding.

A female Members of the Pisauridae family are large hunting spiders whose females carry their spherical egg-sacs under the jaws. The egg-sac is eventually enclosed in a three-dimensional web, called the nursery web, in which the spiderlings will hatch

From "A Guide to Common Singapore Spiders" by Joseph K. H. Koh

BP Guide to Nature Series published by the Singapore Science Centre and sponsored by British Petroleum

© 2000 Joseph K H Koh

Diet choices and influence on behaviour

carnivory

Carnivory (& Insectivory)

- The pressure of competition means:
  - establishing territory
  - prey selection
  - carnivore predation (includes infanticide)
  - cannibalism

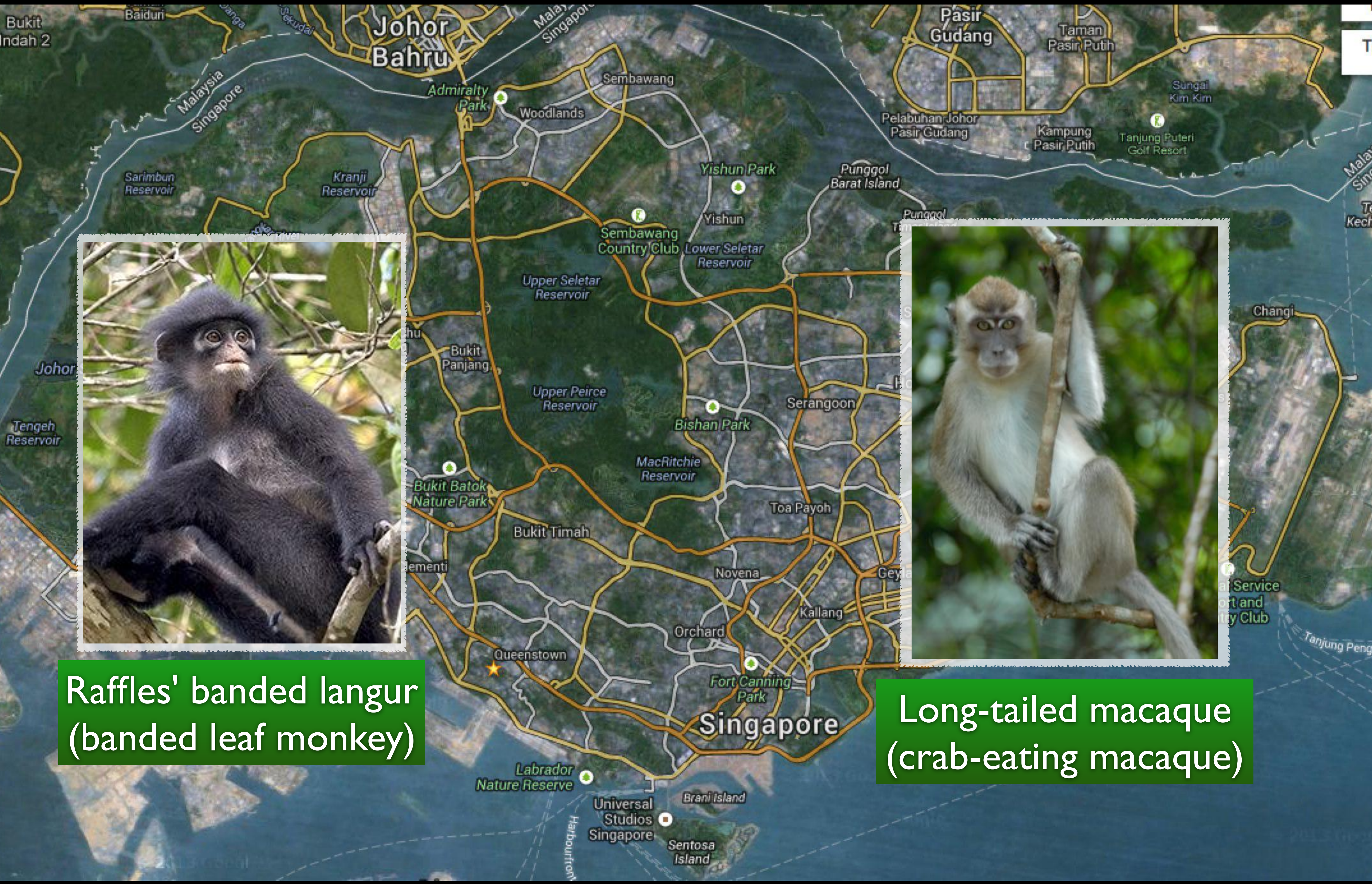
[Derek & Beverly Joubert]

Diet choices and influence on behaviour

omnivory

ix. Omnivory

- Generalists are intelligent, cooperative, exploratory; 'master of none' needs diverse skills, alert to opportunities
- E.g. Compare the behaviour of two primate species in Singapore forests:
  - the long-tailed macaque (urban adaptor)
  - the banded-leaf monkey (urban avoider)



Raffles' banded langur
(banded leaf monkey)

Long-tailed macaque
(crab-eating macaque)

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4. Food handling

4. Food handling

- Carnivory
  - struggling animals
  - suffocate, break/ sever spinal cord
  - inject venom, stalk prey

Komodo dragons (Bull, J.J., T. S. Jessop & M. Whiteley, 2010. Deathly drool: evolutionary and ecological basis of septic bacteria in Komodo dragon mouths. PLoS One, 21;5(6):e11097.

4. Food handling

- Herbivory
  - Overcome defence: chemical, physical methods (herbivory is not passive)
  - Always an arms race between predator and prey

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5. Optimal *Patch* Choice

= Marginal value theorem

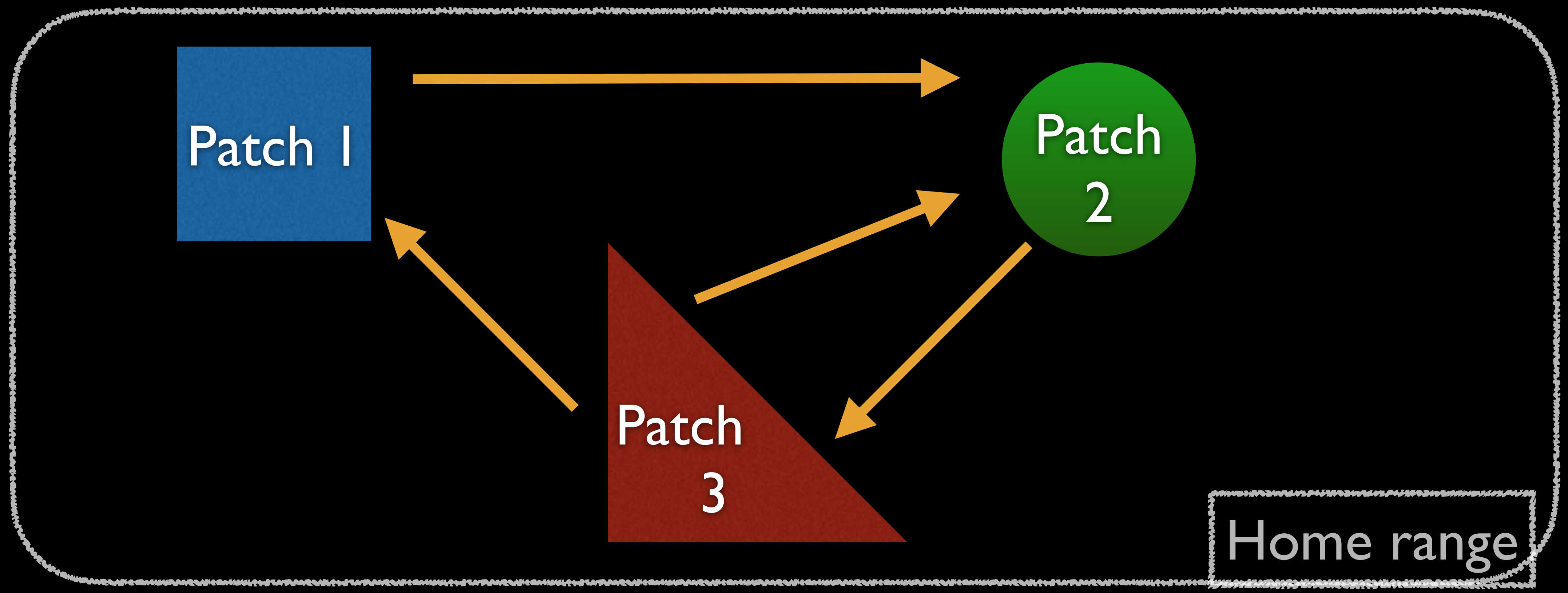
(just one model)

Marginal value theorem

- An optimally foraging individual,
- in a system where resources (typically food)
- are located in discrete patches
- separated by areas with no resources

Optimal Patch Choice

- Where an animal eats (patch choice)
- What it eats when it is there (prey choice)

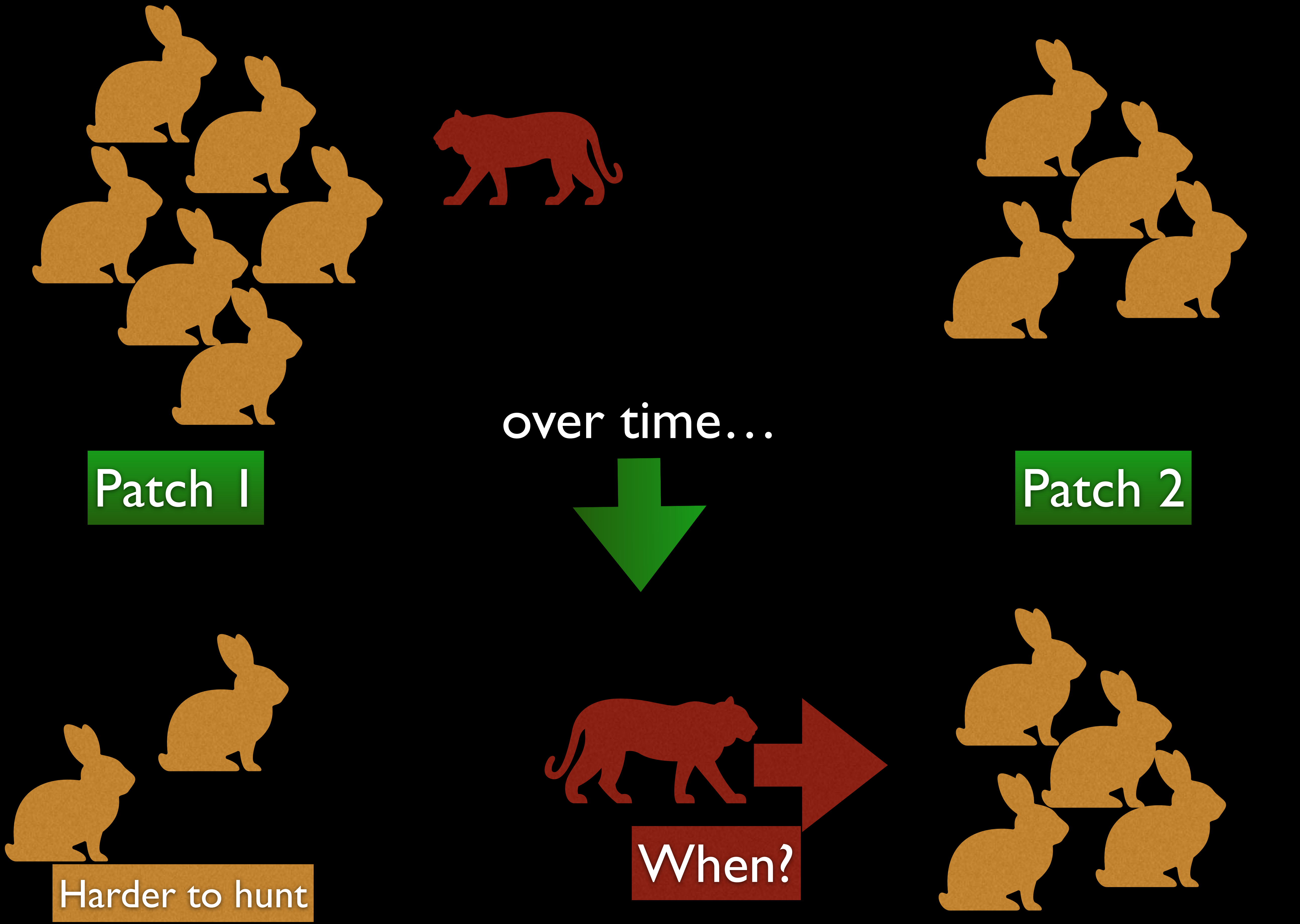


5. Optimal Patch Choice

- Prey (food) is not uniformly distributed (heterogenous or a "patchy" environment)
  - As an animal forages, how long will it stay at a specific patch?
  - How well does it know that patch?
    Remember latent learning? An animal appears to learn without immediate obvious reward such as familiarity with terrain

Moving to the next foraging patch

- When an animal arrives at a particularly rich patch and stays there,
- the value of the patch (e.g. prey density) will eventually diminish.
- At some point, the patch becomes less attractive, and the animal moves on…


over time…
Patch 1
Patch 2
Harder to hunt
When?

Factors in Charnov's marginal value theorem

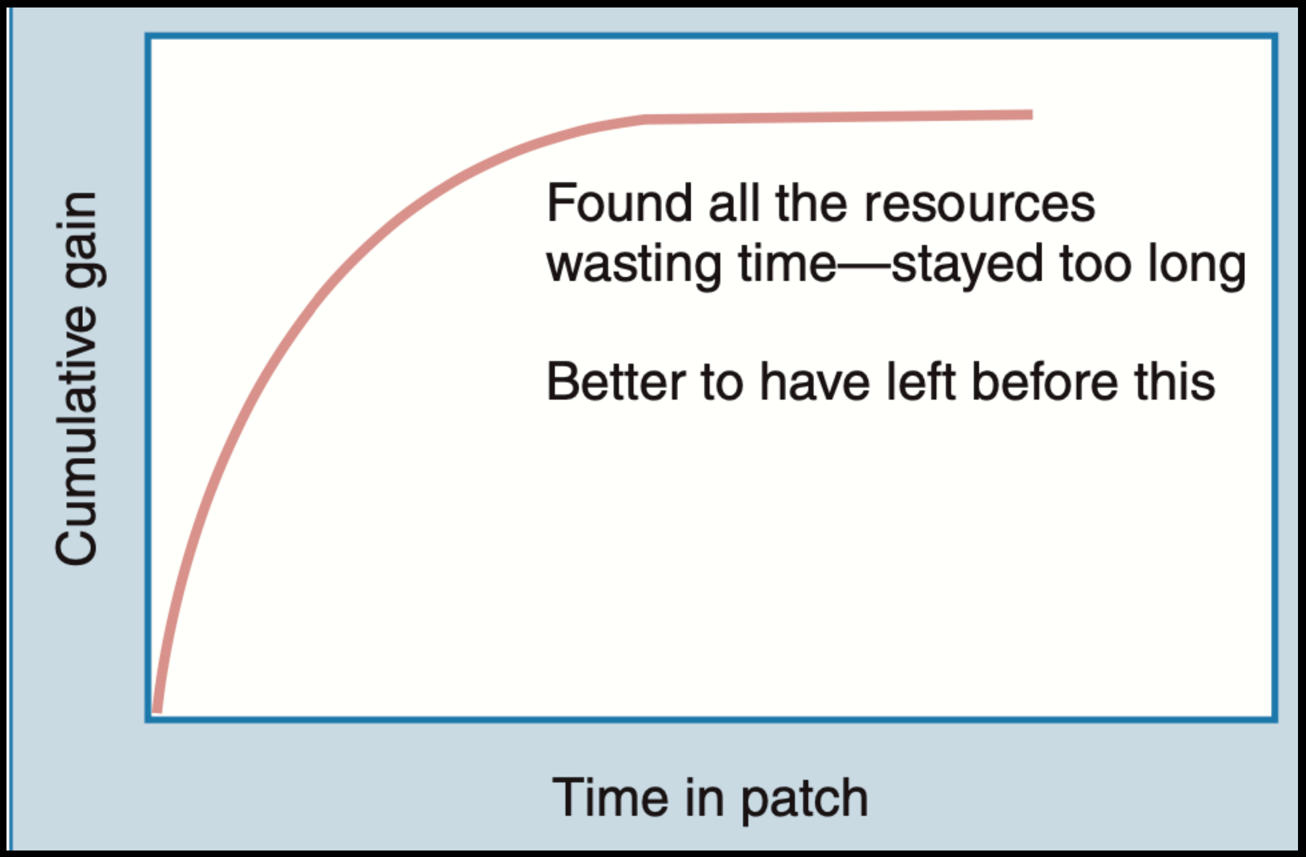
- Animal moves on when the energy gain from the current patch is no longer high (equals average gain from environment)
- If travel time to the next patch is higher, a slower energy gain will be tolerated before the animal moves on (i.e. patch residence increases)

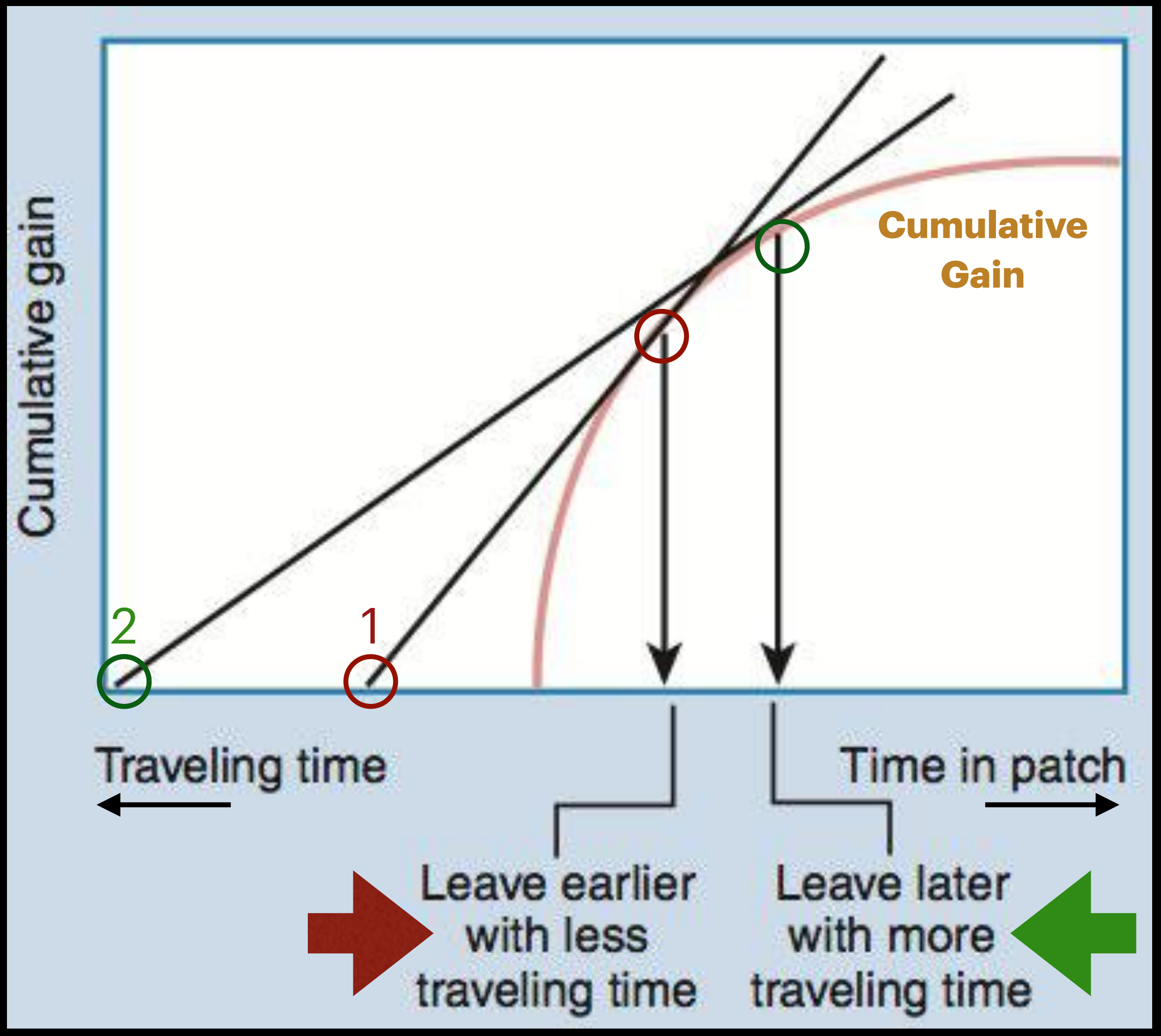
Factors in Charnov's marginal value theorem

Patch residence

- Energy gain drops to average, move on
- Energy gain drop to average, but next patch is poor, stay longer

5. Optimal Patch Choice





When to leave a patch?

5. Optimal Patch Choice

- Marginal value theorem predicts an animal moving from patch to patch is influenced by:
  - average richness of the patches in the area
  - distance to the nearest patch that equals the current one in richness

5. Optimal Patch Choice

- Chipmunks stuff cheeks longer as distance between seed tray and burrow increased
- Patch residence times correlate with patch quality – better food: stay longer
- But there are other factors which influence this, e.g. perceived risk, nutrients instead of just energy, learning, how much an animal monitors other patches.

M. A. Bowers, J. L. Jefferson and M. G. Kuebler, 1993. Variation in Giving-Up Densities of Foraging Chipmunks (*Tamias striatus*) and Squirrels (*Sciurus carolinensis*). Oikos, 66 (2): 229-236

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6. Optimal *Prey* Choice

6. Optimal Prey Choice

- Food is not uniformly presented (variable sizes and location of a prey population)
  - E.g. A forager searching for food which encounters two kinds of food
  - Will it eat every prey item it discovers or
  - will it ignore some to focus on the more rewarding prey?

6. Optimal Prey Choice

Tony Sutton, 2012

Goss-Custard, J. D. (1977). Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Animal Behaviour*, *25*, 10-29.

$$P = \frac{E}{(H + S)}$$

- We assume every animal decides to maximise energy gain (fastest)
- Consider profitability of prey, P
    - = amount of energy obtained from prey
    - ÷ time taken to eat prey (handling)
    - ÷ time taken to find the prey (search)

6. Optimal Prey Choice

Goss-Custard, J. D. (1977). Optimal foraging and the size selection of worms by redshank, *Tringa totanus*, in the field. *Animal Behaviour, 25*, 10-29.

$$P = \frac{E}{(H + S)}$$

- Is $P_{[prey\ 1]} > P_{[prey\ 2]}$?
- Redshank birds were selecting for larger worms which were relatively uncommon, ignoring smaller worms
- Theory predicts well for immobile prey, some factors not considered.

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7. Avoiding predation

Baboons escape lions up a tree in the Kalahari desert, South Africa [Charles J Sharp, 2013]

7. Avoiding predation

- Baboons in a multiple-habitat environment spend 92-97% of their time on food gathering
  - 10% riverbed (resource poor)
  - 90% food found in woodlands (abundant)
  - But predators in the area = leopard and lions (ambush predators, effective in woodlands)

Semen Gondar, Amhara, Ethiopia,by hhesterr, 2012

Tim Ellis, 2012

Cowlishaw, G., 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour,* **53**: 667-686.
Cowlishaw, G., 1997. Refuge use and predation risk in a desert baboon population. *Animal Behaviour,* **54**: 241-253.

7. Avoiding predation: trade offs

Danger:

- Feeding, travelling >> resting, grooming

Open terrain:

- Benefit: difficult for predator to ambush
- Cost: habitat lacks food quantity/quality

7. Avoiding predation: trade offs

What could baboons do?

- Avoid dangerous places
- Avoid dangerous times
- Increased vigilance
- Select portable food

Baboons @ Semen Gondar, Amhara, Ethiopia,by hhesterr, 2012

What do baboons do?

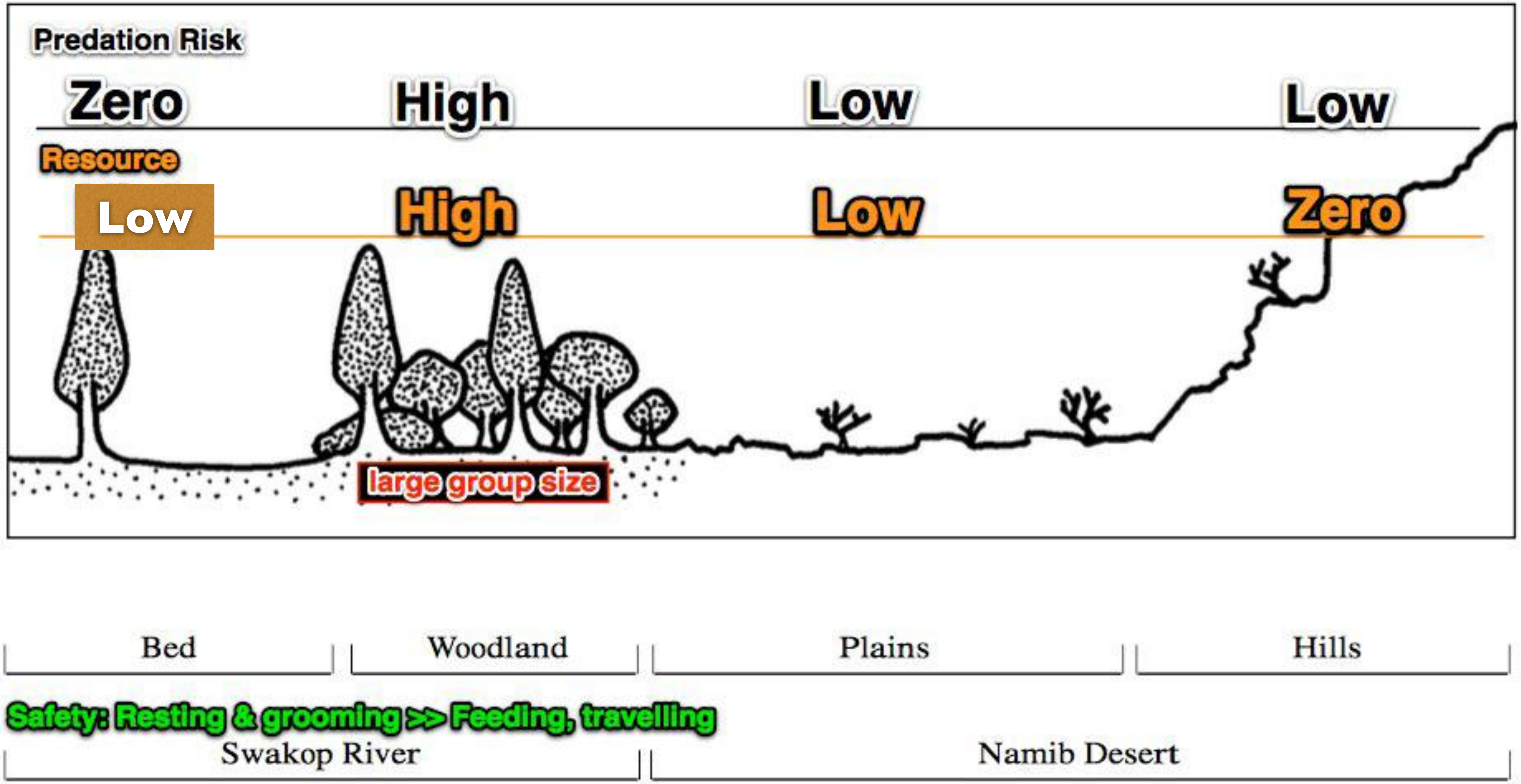


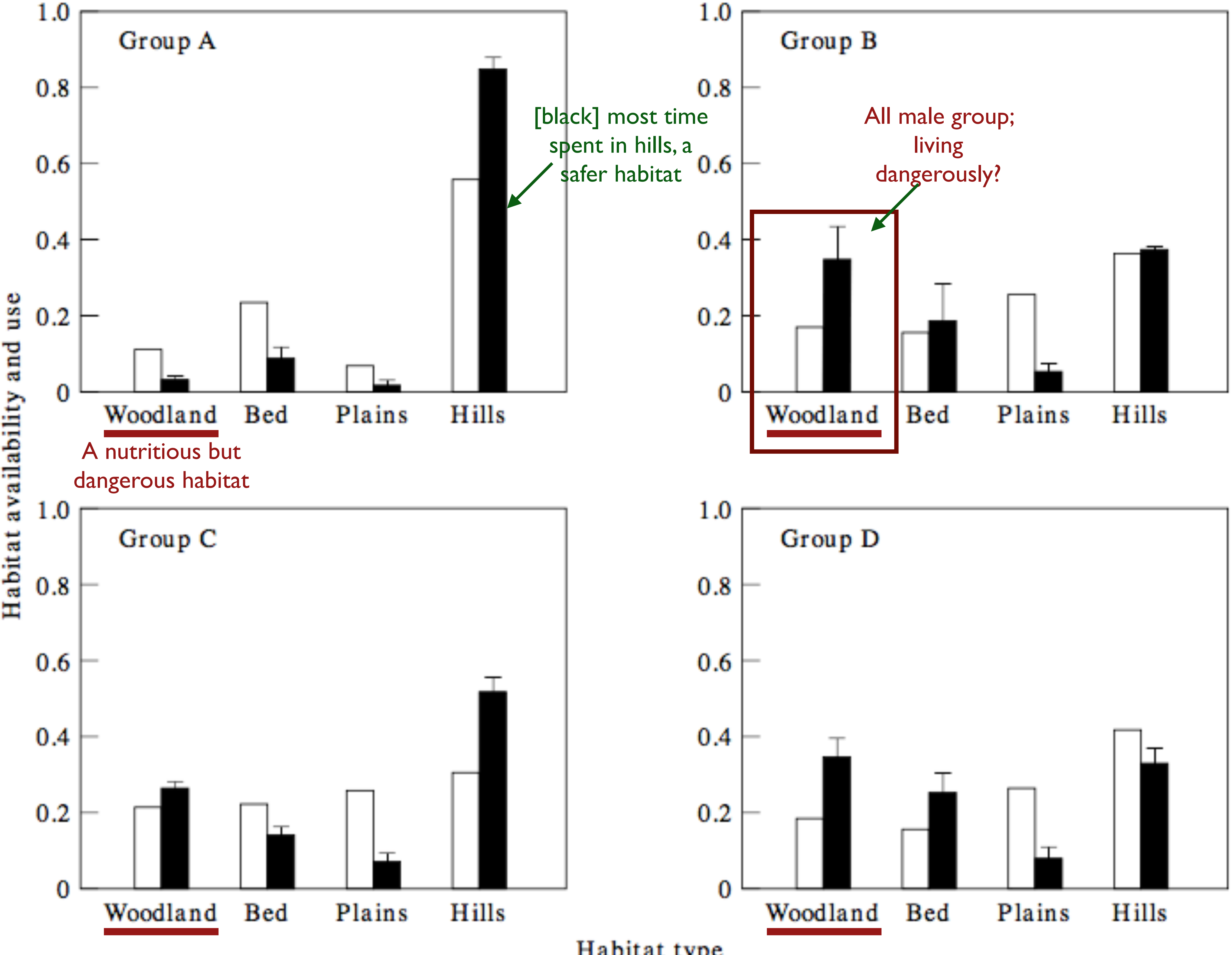
Figure 1. Cross-sectional view of Tsaobis habitats illustrating the variation in vegetation structure and geomorphology across the four habitats and two regions identified.

Cowlishaw, G., 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour,* **53**: 667-686.
Cowlishaw, G., 1997. Refuge use and predation risk in a desert baboon population. *Animal Behaviour,* **54**: 241-253.

Woodlands: good food but also high risk

"the baboons spent less time feeding in the high-risk food-rich habitat but more time feeding in the low-risk relatively food-poor habitat"

Cowlishaw, G., 1997. Refuge use and predation risk in a desert baboon population. Animal Behaviour, 54: 241-253.



igure 2. Proportion of each habitat type in the winter home range (□) and the proportion of individual time $\bar{X} \pm$ SE) spent in the different habitats for each group (■).

Olive baboon (*Papio anubis*) with baby,
Queen Elizabeth National Park, Uganda
[Charles J Sharp, 2016]

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8. Impact of a predator on the ecosystem

Impact of top predator on an ecosystem: The returned wolves of Yellowstone (4:17)