Social and Ecological Determinants of Fission-fusion Sociality in the Spotted Hyena

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Continuum of sociality

**Solitary**
- Alone except when breeding
- Pairs (& their extended families)
- Stable groups, members spend much time alone or in small subgroups

**Obligately gregarious**
- Individuals in cohesive groups unable to survive on their own

Continuum of mammalian sociality

- **Asocial**
  - Black-backed jackals
  - Aye Ayes

- **Eusocial**
  - Giraffe
  - African elephants
  - Naked mole rats

Website: www.msu.edu/user/smith780, Email: smith780@msu.edu
Most carnivores are solitary

69 out of 270 species of carnivores gregarious

65 (94%) species of gregarious carnivores live in fission-fusion societies

- Alone except when breeding
- Pairs (& their extended families)
- Stable groups, members spend much time alone or in small subgroups
- Individuals in cohesive groups unable to survive on their own

Fission-fusion societies

1) Group members know each other as individuals
2) Group members share a common territory
3) Group members rarely, if ever, occur together concurrently; Subgroup sizes and compositions variable
4) Individuals separate regularly, engage in reunion displays

Arnason et al. 2002
1) Spotted hyenas live in large, stable social groups called ‘clans’

Clans are fission-fusion societies

Clans contain multiple matrilines (adult females and their offspring)

Clans contain multiple matrilines and immigrant males
Adult females dominant to immigrant males

Loser of fights

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Breeding females

Immigrant males

Clan members share a communal den where young are socialized

Maintain territory boundaries during border patrols
Cooperatively defend territory during ‘clan wars’ against neighboring clans

Cooperatively defend food from lions

Hyena = 45-86 kg

Lion = 130-260 kg

Clans are fission-fusion societies

3) Individuals occur in subgroups of variable size and composition

Subgroup size = 1
Subgroup size = 2
Subgroup size = 6
Subgroup size = 18

4) Often alone and engage in displays during subgroup reunions

‘Greeting ceremony’
Fission-fusion sociality in spotted hyenas

1) Describe fission-fusion sociality in this species
2) Evaluate circumstances promoting subgroups of various sizes to form
3) Test hypotheses suggesting factors limiting subgroup size

Long-term study (1988-present)
Masai Mara Reserve, Kenya

Data collection methods:
1) Observation sessions
2) Long-term focal surveys

Behavioral data collection

Long-term focal animal surveys for a total of 24 hrs (N =11 females, 9 males)

Fission-fusion sociality in spotted hyenas

1) Describe fission-fusion sociality in this species
   a) Over the course of the day
   b) Frequency of subgroup sizes
   c) As a function of life history stage and social rank
Subgroup size changed many times within a day

![Graph showing subgroup size changes over time](image)

- Changes in subgroup size: $26 \pm 3$/day
- % of clan met/hour: $5.1 \pm 0.6$

Measures of fluidity from long-term follows

![Image of spotted hyena](image)

- Clan size: 28-41

Mean values

**Mara hyenas**
- Subgroup size = 4
- Subgroup duration = 56 min
- % time spent alone = 29%

**Tai chimpanzees**
- Subgroup size = 6
- Subgroup duration = 25 min
- % time spent alone = 18%

(* data obtained or extrapolated from Lehmann et al 2004)

Fission-fusion sociality in spotted hyenas

1) Describe fission-fusion sociality in this species
   a) Over the course of the day
   b) Frequency of subgroup sizes
   c) As a function of life history stage and social rank
Members of the Talek clan were seen alone or in subgroups of various sizes

Mean subgroup size: 3.7

% of observations declined with increasing subgroup size

Clan size: mean = 57 ± 3 (range: 39-74)  
N = 34,850 sessions

Fission-fusion sociality in spotted hyenas

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Life history of the spotted hyena

- Natal den
- Communal den (~13-14 mo)
- Weaning (~24 mo)
- Puberty (males)
- Reproduction (females)
- Join a new clan (males)
Tendency to be alone increased as function of life history stage

Kruskal-Wallis Test Statistic = 422.5, 8 d.f., \( P < 0.0001 \)

Low-ranking hyenas spent more time alone than did high-ranking ones

Females: \( R_s = 0.77, N=24 \) ranks, Males: \( R_s = 0.85, N=18 \) ranks

\( P < 0.00001 \) for both

Fission-fusion sociality in spotted hyenas

1) Describe fission-fusion sociality in this species

2) Evaluate circumstances promoting subgroups of various sizes to form

Assigned each session to a single context
Subgroup size varied by context

Kruskal-Wallis $H_{8,34847} = 11030.49, P < 0.0001$

Typical kill scene: Predator (60kg) vs. Prey (180kg)

Kruskal-Wallis $H_{8,34847} = 11030.49, P < 0.0001$
Subgroup size varied by context

Kruskal-Wallis $H_{8,34847} = 11030.49, P < 0.0001$
Fission-fusion sociality in spotted hyenas

1) Describe fission-fusion sociality in this species
2) Evaluate circumstances promoting subgroups of various sizes to form
3) Test hypotheses suggesting factors limiting subgroup size
   a) Ecological constraints hypothesis
   b) Infant safety hypothesis
   c) Dispersive conflict resolution hypothesis

Ecological constraints hypothesis (Chapman 1990)

Competition for limited resources constrains gregariousness

Intense within-group competition over rich food resources that are ephemeral and usurpable

If feeding competition limits gregariousness, then:
1) Feeding success should decline with subgroup size and low-ranking animals should suffer most from this decline
Energy gain decreases as the number of hyenas at kills increases

\[ R_s = -0.71, P < 0.0001 \]

Social rank determines feeding success

\[ R_s = -0.60, N = 24 \text{ rank positions, } P = 0.002 \]
\[ R_s = -0.70, N = 14 \text{ relative ranks, } P = 0.006 \]

Ecological constraints hypothesis

If feeding competition limits gregariousness, then:

2) Individuals should congregate at food sources in numbers proportional to patch richness

Thomson’s gazelle (25 kg)
Impala (53 kg)
Topi (119 kg)
Wildebeest (132 kg)
Zebra (235 kg)
Giraffe (935 kg)
Elephant (3,550 kg)

Increasing patch richness

(Kingdon 1997, Oindo 2002)
Numbers of hyenas at kill scenes proportional to the prey size

Ecological constraints hypothesis

If feeding competition limits gregariousness, then:

3) Individuals should spend more time with conspecifics

Biweekly prey census

Hyenas most gregarious during months of superabundant prey

Counts all prey 100 m of two 4-km transect lines

Mann-Whitney $U = 4783.5$, $P < 0.001$

$N = 122$ low and $60$ high prey months

$R_s = 0.98$, $N = 8$ prey types, $P < 0.0001$
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Infant safety hypothesis

Infanticide occurs in hyenas

(Kruuk, 1972; East & Hofer, 2002; White, 2005)

Infant safety hypothesis

If the risk of infanticide limits gregariousness, then:

1) Females should spend the most time away from conspecifics when she is close to parturition

Females living in FF societies might avoid group members to reduce the risk of infanticide
Infant safety hypothesis

If the risk of infanticide limits gregariousness, then:

2) Mothers should be seen most often with offspring during the most vulnerable life history stages

Fission-fusion sociality in spotted hyenas

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Dispersive conflict resolution hypothesis (Schino, 2000)

Might help hyenas avoid the costs associated with aggression

Conclusions

Fission-fusion societies of spotted hyenas are highly flexible

Between group competition: is a cohesive force, promoting large subgroup sizes to form

Within group competition: is a disruptive force, promoting the tendency for hyenas to be alone

Acknowledgements

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Spotted hyenas often alone

But...energy gain increases with pack size in wild dogs living in cohesive groups

Holekamp et al. 2000

Spotted hyenas hunt by coursing

Number of companions

Consecutive days sighted

Energy gain (kJ/female/day)

Number of adult females

Creel 1997
Number of males observed with females increases as females approach estrus

Maternal rank ‘inheritance’

Youngest ascendancy

Murphy...........................................1
Artemis..............2
Athena............3
Seinfeld.................................4
Whoopie.................................5