Clever mothers balance time and effort in parental care – a study on free-ranging dogs

Manabi Paul\textsuperscript{1}, Shubhra Sau\textsuperscript{1}, Anjan K. Nandi\textsuperscript{2} and Anindita Bhadra\textsuperscript{1}\textsuperscript{*}

\textsuperscript{1} Behaviour and Ecology Lab, Department of Biological Sciences,
Indian Institute of Science Education and Research – Kolkata, India

\textsuperscript{2} Department of Physical Sciences,
Indian Institute of Science Education and Research – Kolkata, India

\textsuperscript{*}Address for Correspondence:

Behaviour and Ecology Lab, Department of Biological Sciences,
Indian Institute of Science Education and Research – Kolkata
Mohanpur Campus, Mohanpur,
PIN 741246, West Bengal, INDIA

tel. 91-33-25873119
fax +91-33-25873020

e-mail: abhadra@iiserkol.ac.in
### Active maternal care

| Code | Behaviour          | Description of the behaviour                                                                 |
|------|--------------------|---------------------------------------------------------------------------------------------|
| AG   | Allo groom         | To clean the coat of their pups by licking, to remove dirt and parasites.                    |
| CK   | Nursing            | To lie down or stand still in order to allow pups to suckle (feed on breast milk).          |
| EF   | Eat fecal matter   | Mother eats fecal matter of her pups to clean her den.                                       |
| OF   | Offer food         | Mother brings food obtained through scavenging/begging in her mouth and drops it on the ground in the vicinity of the pups, allowing them to eat. |
| PL   | Play               | Individuals engage in affiliative activities like bowing down, tail wagging, mock biting, jumping, tumbling, etc. for enjoyment. |
| PS   | Pile sleep         | Individuals pile up together while sleeping ensuring maximum body contact.                   |
| PU   | Pile Up            | Individuals pile up together while resting ensuring maximum body contact.                    |
| TH   | Threat             | Individuals assume an aggressive posture with raised tail and ears, exposed jaws, fore legs stretched forward, producing a deep throated growl and staring at the recipient for a prolonged time. |
| VM   | Vomit              | Expels the semi digested and semi solid contents of stomach by regurgitation.               |

### Passive maternal care

| Code | Behaviour | Description of the behaviour |
|------|-----------|-----------------------------|
A table showing the ethogram for maternal care. A unique two letter code was used for recording each behaviour during observations. The table shows the code, the name of the behaviour and its description. Maternal care was divided into active and passive care. Active care behaviours involved direct social interactions between the mother and pups. The passive care behaviours were not interactions, but individual actions of the mother occurring in the vicinity of the pups which allowed them to share time and space with and provide protection to the pups.

In case of social interactions, the individual starting the interaction was designated as the initiator and the one towards which the behaviour was shown, was the recipient (Please see Martin and Bateson 2007 *Measuring Behaviour: An Introductory Guide*, 3rd edn. Cambridge University Press).

(*) see Bhadra et al. 2016 for different types of food eaten by free-ranging dogs.

| Code | Behaviour                | Description                                                                 |
|------|--------------------------|-----------------------------------------------------------------------------|
| DW   | Drink water              | Individuals drinking water from sources like puddles, shallow drains, dripping taps, etc. |
| ET   | Eating food              | Individuals feeding on any solid or semi-solid food items.                  |
| FS   | Food search              | Individuals wander around and search thoroughly (by using the visual, olfactory or tactile cues) for food*. |
| GR   | Groom                    | Individuals clean their own bodies by licking, to remove dirt and parasites. |
| LG   | Scratching by legs       | Individuals use their claws while sitting or standing, to scratch themselves. This is a self-maintenance behaviour. |
| LI   | Licking                  | Individuals pass their tongue over their body to make it clean.             |
| OT   | Resting/ standing/ lazing| Individuals sit, stand or lie down and remain immobile for several (at least 2) minutes at a stretch. |
Details of the linear mixed effect model that shows the effect of pup age and their current litter size on the proportion of time spent in total care by the mother.

In order to check the effect of both the predictor variables i.e. pup age and mother’s current litter size, we ran a “linear mixed effect model” incorporating the predictor variables as the “fixed effects” whereas the proportion of time spent by the mother in total care was included in the model as the “response variable”. We collected the data on maternal care from 15 different dog groups that have 22 mother-litter units, over a span of 5 years (2010-2015). Hence the identity of each mother-litter units (fgr) and the year of data collections (fyr) were incorporated in the model as the “random effects”. A Gaussian distribution was considered for the response variable in the model. We started with the full model (mod1), i.e., with all possible two-way interactions among the fixed effects.

Variables used in the model:

Response variable:
Proportion of time spent by the mother in total care- **totpcprop**

Fixed effects:
Age of pups in weeks- **age**
Current litter size- **LS**

Random effects:
Mother-litter unit’s identity- **fgr**
Year of observation- **fyr**

Model: **mod1<- lme (totpcprop ~ age*LS, random = ~1|fgr/fyr)**

| Value | Std. Error | DF | t-value | p-value |
|-------|------------|----|---------|---------|

Results
The two-way interaction shown no significant effect on the response variable and hence we reduced the model using standard protocol of backward selection method and ended up with the optimal model (mod2).

Model: `mod2 <- lme(totpcprop ~ age + LS, random = ~1|fgr/fyr)`

Results

|          | Value   | Std. Error | DF    | t-value | p-value |
|----------|---------|------------|-------|---------|---------|
| (Intercept) | 0.9774950 | 0.11531726 | 169   | 8.476572 | 0.0000  |
| age      | -0.0218620 | 0.01003326 | 169   | -2.178953 | 0.0307  |
| LS       | -0.0987305 | 0.02951282 | 169   | -3.345342 | 0.0010  |
| age*LS   | 0.0037576 | 0.00284882 | 169   | 1.318992 | 0.1890  |
Details of the linear mixed effect model that shows the effect of pup age and their current litter size on the proportion of time spent in active care by the mother.

The predictor variables i.e. the “age” and “LS” were incorporated in the generalized linear mixed effect model to check their effect on the response variable i.e. the proportion of time spent in active care (acareprop) for 22 mother-pups unit, collected over a span of 5 years. Identity of each mother-pups unit (fgr) and the year of data collections (fyr) were added in the model as the “random effects”. We started with the full model (mod3), i.e., with all possible two-way interactions among the fixed effects.

Model validation

Since the residuals have an essential role in the model validation process, we did the “Bartlett test of homogeneity” of variances to check the presence of homoscedasticity in the model, separately for two predictor variables i.e. pup age (age) and current litter size (LS). P-value for the predictor “age” exhibited violation in the homogeneity assumption and it was fixed by adding “varFixed” as the “weight” in the model.

Variables used in the model:

Response variable:
Proportion of time spent by the mother in active care- acareprop

Fixed effects:
Age of pups in weeks- age
Current litter size- LS

Random effects:
Mother-litter unit’s identity - fgr
Year of observation- fyr

Model: mod3<- lme(acareprop ~ age * LS, random= ~1|fgr/fyr, weights= varFixed(~age))
## Results

|          | Value      | Std. Error  | DF  | t-value | p-value |
|----------|------------|-------------|-----|---------|---------|
| (Intercept) | 1.0513085 | 0.09673973  | 169 | 10.867392 | 0.0000  |
| age      | -0.0799352 | 0.00898196  | 169 | -8.899528 | 0.0000  |
| LS       | -0.1216618 | 0.02361754  | 169 | -5.151332 | 0.0000  |
| age*LS   | 0.0092408  | 0.00257809  | 169 | 3.584355  | 4e-04   |

Here the two-way interaction between the age and LS shown significant effect on the response variable and hence we kept this model.
Details of the linear mixed effect model that shows the effect of pup age and their current litter size on the active care received per pup.

Total active care shown by the mother for a particular group was divided equally among the pups that were observed to present for the respective week of pup age. Active care received per pup was incorporated into the generalized linear mixed effect model as the response variable. We wanted to check the effect of predictor age and LS on the amount of active care received per pup. Identity of each mother-pups unit (fgr) and the year of data collections (fyr) were added in the model as the “random effects”. We started with the full model (mod4), i.e., with all possible two-way interactions among the fixed effects.

Model validation
Since the residuals have an essential role in the model validation process, we did the “Bartlett test of homogeneity” of variances to check the presence of homoscedasticity in the model, separately for two predictor variables i.e. pup age (age) and current litter size (LS). P-value for the predictor “age” exhibited violation in the homogeneity assumption and it was fixed by adding “varFixed” as the “weight” in the model.

Variables used in the model:

Response variable:
Active care received per pup- acareperpup

Fixed effects:
Age of pups in weeks- age
Current litter size- LS

Random effects:
Mother-litter unit’s identity- fgr
Year of observation- fyr

Model: mod4<- lme(acareperpup ~ age * LS, random= ~1|fgr/fyr, weights= varFixed(~age))
Results

|       | Value      | Std. Error | DF  | t-value    | p-value |
|-------|------------|------------|-----|------------|---------|
| (Intercept) | 0.5574674  | 0.04028909 | 169 | 13.836682  | 0.0000  |
| age    | -0.0377047 | 0.00383511 | 169 | -9.831449  | 0.0000  |
| LS     | -0.0905445 | 0.01000378 | 169 | -9.051032  | 0.0000  |
| age*LS | 0.0052365  | 0.00110413 | 169 | 4.923760   | 0.0000  |

Here the two-way interaction between the age and LS shown significant effect on the response variable and hence we kept this model.
Details of the linear mixed effect model that shows the effect of pup age and their current litter size on the proportion of time spent in passive care by the mother.

The predictor variables i.e. the “age” and “LS” were incorporated in the generalized linear mixed effect model to check their effect on the response variable i.e. the proportion of time spent in passive care (pcareprop) for 22 mother-pups unit, collected over a span of 5 years. Identity of each mother-pups unit (fgr) and the year of data collections (fyr) were added in the model as the “random effects”. We started with the full model (mod5), i.e., with all possible two-way interactions among the fixed effects.

**Variables used in the model:**

**Response variable:**
Proportion of time spent by the mother in passive care - pcareprop

**Fixed effects:**
Age of pups in weeks - age
Current litter size - LS

**Random effects:**
Mother-litter unit’s identity - fgr
Year of observation - fyr

**Model:** mod5<- lme(pcareprop ~ age * LS, random= ~1|fgr/fyr, weights= varFixed(~age))

**Results**

|        | Value     | Std. Error | DF    | t-value  | p-value |
|--------|-----------|------------|-------|----------|---------|
| Intercept | 0.05735617 | 0.08746429 | 169   | 0.655767 | 0.5129  |
| age     | 0.04428560 | 0.00786539 | 169   | 5.630439 | 0.0000  |
The two-way interaction shown no significant effect on the response variable and hence we reduced the model using standard protocol of backward selection method and ended up with the optimal model (mod6).

Model: $ \text{mod6}< \text{lme(pcareprop} \sim \text{age} + \text{LS}, \text{random= } \sim 1|\text{fgr/yr}, \text{weights= varFixed(} \sim \text{age)} $

Results

|          | Value    | Std. Error | DF   | t-value  | p-value  |
|----------|----------|------------|------|----------|----------|
| (Intercept) | 0.05735617 | 0.08746429 | 169  | 0.655767 | 0.5129   |
| age      | 0.04428560 | 0.00786539 | 169  | 5.630439 | 0.0000   |
| LS       | 0.00443542 | 0.02273035 | 169  | 0.195132 | 0.8455   |
Details of the linear mixed effect model that shows the effect of pup age and their current litter size on rate (frequency per hour) of care received (in terms of suckling and allogrooming) by individual pups.

The predictor variables i.e. the “age” and “LS” were incorporated in the generalized linear mixed effect model to check their effect on the response variable i.e. the rate of (frequency per hour) of care received (in terms of suckling and allogrooming) by individual pups (carercvd) for 22 mother-pups unit, collected over a span of 5 years. Identity of each mother-pups unit (fgr) and the year of data collections (fyr) were added in the model as the “random effects”. We started with the full model (mod7), i.e., with all possible two-way interactions among the fixed effects.

**Variables used in the model:**

**Response variable:**

The rate of (frequency per hour) of care received (in terms of suckling and allogrooming) by individual pups - carercvd

**Fixed effects:**

Age of pups in weeks- age

Current litter size- LS

**Random effects:**

Mother-litter unit’s identity - fgr

Year of observation- fyr

Model: mod7<- lme(carercvd ~ age * LS, random= ~1|fgr/fyr)
## Results

|        | Value  | Std. Error | DF  | t-value | p-value   |
|--------|--------|------------|-----|---------|-----------|
| (Intercept) | 9.61189 | 0.91536    | 169 | 10.501  | 2.22e-16  |
| age    | -0.73337 | 0.08936    | 169 | -8.207  | 6.66e-14  |
| LS     | -1.12415 | 0.23868    | 169 | -4.710  | 7.24e-06  |
| age*LS | 0.08342  | 0.02542    | 169 | 3.282   | 0.00124   |