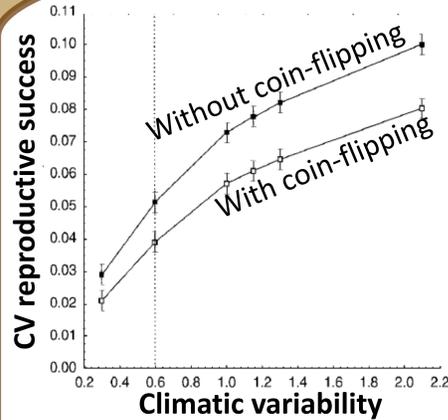


## Context

**Bet-hedging strategies** are a response to a **variable** environment characterized by **unpredictable conditions**.

**Coin-flipping** is one type of bet-hedging strategy, in which an increase of the phenotypic **variance of offspring** within a generation leads to a decrease in the variance of **reproductive success** of parents [1, 2].

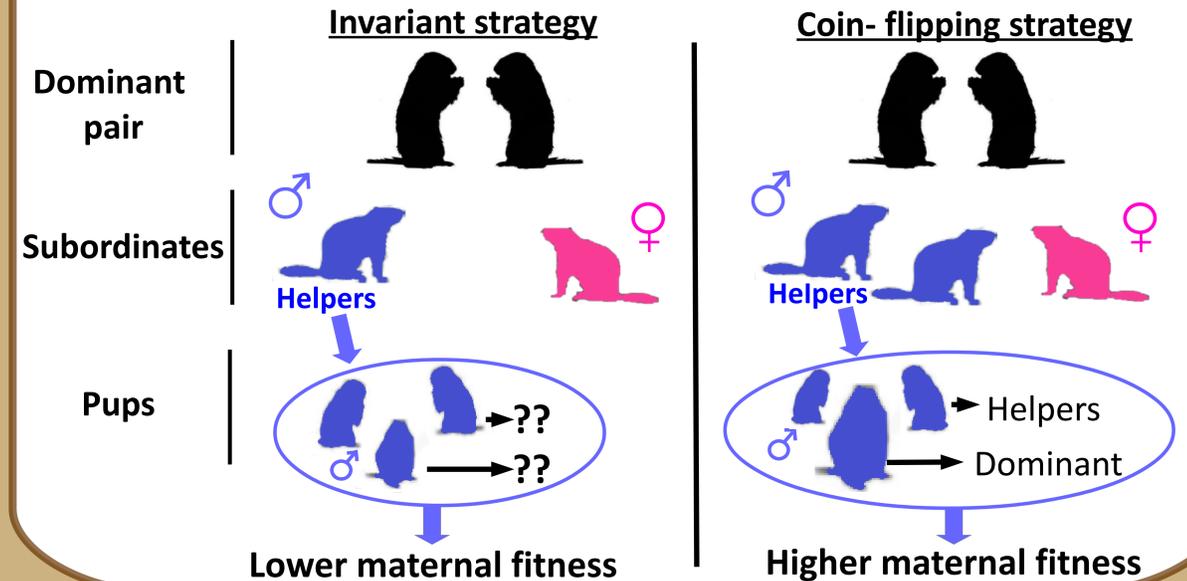
**Cooperative breeding** is a social system commonly encounter in unpredictable environments. In this social system, **helpers** forgo their own reproduction to **assist reproductive pairs** in raising their offspring. Cooperative breeding may favor coin-flipping strategy [6]: In cooperative breeders, mothers producing offspring of variable size within a litter (coin-flipping strategy) should have **higher fitness** than mothers producing **offspring of uniform size** (invariant strategy) [3,4] (fig. 1).



**Fig 1.** Coefficients of variation (CV) of reproductive success according to different strategies [5].

## A test in Alpine marmots

The **Alpine marmot** (*Marmota marmota*) is a **cooperative breeder** living in an **unpredictable mountain environment**.

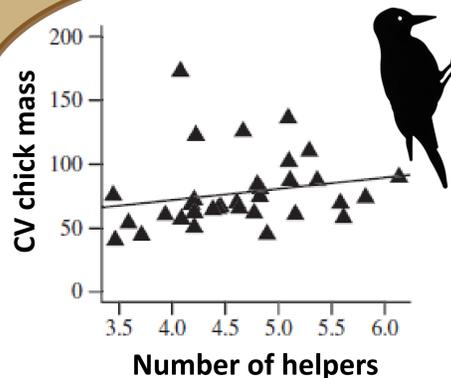


## Hypotheses

(1) The **number of helpers** should impact the **coin-flipping strategy** : ↑ nb of helpers : ↑ intra-litter **variance**

(2) Following a **coin-flipping strategy** should be rewarding in terms of **maternal fitness**

## State of the Art



**Fig 2.** Coefficient of variation of chick mass as a function of helper number in acorn woodpecker (*Melanerpes formicivorus*) [6].

Empirical studies have evidenced different coin-flipping strategies in cooperative breeding vertebrates and invertebrates. However, a single empirical test, conducted on acorn woodpecker, shows **an increase in the variance of offspring mass in groups with more helpers** (fig. 2). And, to the best of our knowledge, **no study has tested for a link between coin-flipping and offspring performance or maternal fitness**.

This gap stems from the difficulty to have appropriate measure of maternal fitness over a sufficient number of individuals [7]. This difficulty is even more acute when it comes to cooperative breeders since, in such species, an individual **inclusive fitness** is the sum of its **direct fitness** (*i.e.* genes transmitted to the next generation though its own reproduction) and **indirect fitness** (*i.e.* genes transmitted to the next generation though the reproduction of its kins) [7].

**How can we measure the inclusive fitness of each mother?**

Direct fitness



**Geometric mean of the recruitment rates**

Indirect fitness



**Effect of helpers on the recruitment rates**

## Analyses

**Characterisation of the coin-flipping strategy**

Coefficient of variation (CV) of the body mass of males in each litter

$$CV = \frac{\text{Standard deviation}}{\text{Mean}} \times 100$$

(1) **Effect of helpers**

(2) **Effect on fitness**

Use of **Mixed model**  
Explanatory variable

**Number of helpers**

Confounding factors

- Maternal condition
- Climatic variables
- Litter size
- Random factor : Territory

Use of **Integral projection model**

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