Eurasia Specialized Veterinary Publication

**Entomological Research Letters**

**ISSN: 3108-639X**

2022, Volume 2, Issue 1, Page No: 91-98
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Available online at: www.esvpub.com/

# Reproductive State Reshapes the Balance Between Risk and Reward During Insect Foraging Decisions

**Lukas Weber[1]*, Sophie Janssen[2], Jonas Richter[1], Elena Fischer[3]**

[1]Department of Reproductive Physiology and Foraging Ecology, Faculty of Life Sciences, University of Stuttgart, Stuttgart, Germany.
[2]Department of State-Dependent Risk Assessment, Faculty of Biosciences, Eindhoven University of Technology, Eindhoven, Netherlands.
[3]Department of Insect Decision-Making and Reward Systems, Faculty of Sciences, University of Basel, Basel, Switzerland.

***E-mail** ✉ lukas.weber@uni-stuttgart.de

**ABSTRACT**

Insect foraging decisions are commonly interpreted through energetic demand, resource quality, and environmental risk, yet reproduction changes both what resources are worth and what costs can be tolerated. Treating reproductive state as a single scalar such as mating status or egg load obscures this conditionality. Evidence across insects shows that mating, nutritional state, egg limitation, resource quality, predation, sexual interference, and future reproductive opportunity can each alter behavior, but they are rarely integrated within the same decision architecture. This article proposes that reproductive state is a multidimensional decision variable that can reshape a qualitative risk–reward surface rather than uniformly increasing or decreasing risk-taking. Immediate resource value, remaining reproductive opportunity, and exposure cost are treated as analytically distinct currencies whose relative influence can change with sex, life stage, ovigeny, social context, and environmental history. The theory predicts conditional, potentially nonmonotonic responses: identical hazards or resources need not produce identical behavior in different reproductive states, and the same state proxy need not predict behavior across taxa. The framework is intended as a falsifiable synthesis, not a validated universal mechanism.

**Keywords:** Reproductive state, Insect foraging, Risk-sensitive behavior, Resource valuation, Predation risk, Life-history trade-offs

**Received:** 18 April 2022
**Revised:** 08 June 2022
**Accepted:** 09 June 2022

**How to Cite This Article:** Weber L, Janssen S, Richter J, Fischer E. Reproductive State Reshapes the Balance Between Risk and Reward During Insect Foraging Decisions. Entomol Res Lett. 2022;2(1):91-8. https://doi.org/10.51847/wZLgUtqtyk

## Introduction

Foraging is not merely the acquisition of energy; it is a sequence of choices whose consequences depend on the organism's current state. In *Drosophila*, experimentally defined internal states can alter food choice through distinguishable sensorimotor computations, while in female bed bugs mating and starvation interact in their effects on host seeking and blood feeding [1, 2]. These findings justify a state-dependent account of resource acquisition but also expose a central inferential problem: “reproductive state” cannot be substituted for hunger, arousal, or one reproductive proxy. The theoretical question is therefore not whether reproduction changes foraging, but how reproductive condition changes the relative value of rewards and costs that already structure a foraging decision. A simple egg-load interpretation is insufficient. In the egg parasitoid *Trissolcus japonicus*, locomotor activity can track egg load under some conditions, yet high-quality host patches increase activity after oviposition despite egg depletion [3]. Reproductive limitation therefore does not uniquely determine search effort. Exposure costs are

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similarly heterogeneous. Bumblebee workers differed in anti-predator behavior according to body size and predator context [4]. At a different biological level, complementary resource limitation altered bumblebee colony foraging and reproductive performance [5]. Colony state is informative about social resource demand, but it is not equivalent to the reproductive state of an individual worker or solitary female.

Several literatures consequently contribute different currencies rather than one common response variable. Central-place honeybee foraging demonstrates that spatial and energetic payoffs can structure resource use without invoking personal reproductive state [6]. Parasitoid life-history modeling shows that conditional optima can be represented on multidimensional trade-off surfaces, although that precedent does not validate the surface proposed here [7]. In burying beetles, greater current reproductive allocation can reduce later competitive ability without a parallel detectable survival difference [8]. In ground beetles, predation risk can reduce food choosiness rather than simply suppress foraging [9]. Together, these cases motivate a theory in which immediate reward, future reproductive opportunity, and exposure cost remain distinct.

The contribution developed here is a proposed behavioral architecture in which reproductive state changes the weighting or interpretation of these currencies. It does not assume that reproduction invariably raises risk tolerance, that observed behavior is optimal, or that common molecular mechanisms operate across insect orders. Instead, it asks when reproductive condition should alter resource valuation, when environmental costs should dominate, and when apparently contradictory foraging responses are expected because different state dimensions or decision currencies have been measured.

*Theoretical assumptions*

The first assumption is that resource value is multidimensional and conditional. Spatial and energetic efficiency can organize central-place foraging [6], while theoretical parasitoid work demonstrates that host and food availability can jointly alter life-history solutions on a multidimensional surface [7]. For the present theory, these precedents support a qualitative decision geometry, not a fitted optimization model. “Reward” therefore denotes the state-dependent value of acquiring or exploiting a resource, rather than a universal energetic quantity.

The second assumption is that reproductive state is a vector of partially separable descriptors. Internal states need not influence choice through the same processing locus [1]. Egg load can be behaviorally relevant yet overridden by resource quality [3], and current reproductive allocation can affect a later competitive currency [8]. Mating status, egg load, ovarian activity, recent oviposition, maturation stage, and current reproductive investment should therefore not be assigned numerical equivalence without direct evidence. A simpler latent-motivation explanation remains possible in some systems, but it cannot be assumed across taxa.

The third assumption is that exposure cost has structure independent of reproductive state. Anti-predator responses differ among bumblebee worker phenotypes [4], social resource need can modify worker foraging without representing personal reproduction [5], and predation can alter food selectivity rather than only the probability of foraging [9]. The proposed theory consequently separates state from cost and allows them to interact only when evidence or a testable hypothesis warrants that interaction. This separation is essential: a behavioral change observed after mating is not evidence that perceived danger changed, and a behavioral response to danger is not evidence that reproductive valuation caused it.

*Reproductive state as a decision variable*

Direct mechanistic evidence is strongest in *Drosophila* and shows that reproduction can reconfigure feeding through more than one route. In mated females, a gut-derived hormonal pathway can suppress sugar appetite and regulate food choice, while reproductive-state-specific remodeling of enteric neural control can increase maternal food intake [10, 11]. These experiments support the general behavioral principle that reproductive physiology can alter resource valuation or intake. They do not establish that the same molecular pathways operate in other insects or that the resulting feeding changes represent greater willingness to accept predation risk.

Mating itself can also establish a persistent reproductive behavioral state. Neural circuitry linking mating to egg laying in female *Drosophila* demonstrates persistence in a reproductive decision domain, but it does not show that the same circuit controls food foraging [12]. Nutritional state adds another dimension: internal amino-acid condition modulates yeast taste neurons, while reproductive and nutritional influences on protein appetite remain distinguishable [13]. Time adds a further boundary. Mated females consume more amino acids during the dark phase, and this post-mating feeding effect can occur independently of egg production [14]. Thus, mating, egg

production, nutrient deficit, and time of day cannot be treated as interchangeable indicators of one reproductive drive.

State-dependent sensory tuning and behavioral prioritization provide additional, but deliberately bounded, analogies. After mating, female *Drosophila* become more choosy toward males as olfactory sensitivity to a male pheromone changes [15]. This is evidence that mating can change cue valuation in mate choice, not direct evidence for altered food choice. In males, food deprivation, food quality, and sexual opportunity can reorder the choice between feeding and courtship through identified neuronal processes [16]. That result demonstrates competition among behavioral priorities in a different sex and decision context; it cannot be imported as a female reproductive-state mechanism.

On this basis, the article proposes reproductive state as a dynamic vector with at least three logically separable functions: altering the value assigned to a resource, altering how relevant cues are processed, and altering the opportunity cost of time or effort spent foraging. The exact biological variables representing those functions will differ among insects. In a synovigenic parasitoid, egg availability may be central; in a mated fly, nutrient-specific physiology may dominate; in a provisioning bee, offspring demand and sexual interference may be more consequential. The vector is therefore an organizing construct, not a hidden physiological variable claimed to have been measured.

*Resource value and future reproductive opportunity*

Resource value is also distributed across biological levels. In *Bombus impatiens*, colony provisioning state changes worker foraging motivation over short and longer timescales [17]. Such evidence shows that the value of an additional foraging trip can depend on social resource need, but colony demand must remain analytically external to an individual worker's personal reproductive state. Social insects therefore provide useful tests of contextual valuation while also illustrating a level-of-analysis trap.

For solitary females, resource acquisition may compete directly with reproductive interactions. Female *Anthrenoides micans* reject males while collecting food for offspring; the published reduction in flower visitation under universal mating acceptance is a time-budget counterfactual rather than an observed fitness decrement [18]. The important point is qualitative: mating opportunities and courtship interference can consume time that would otherwise be available for provisioning. A resource can consequently have high nutritional or offspring value while the act of obtaining it carries a reproductive opportunity cost.

Life-history strategy further changes what “future opportunity” means. Age and oviposition history influence resource acceptance differently among pro-ovigenic and synovigenic fig-wasp exploiters [19]. In the synovigenic parasitoid *Copidosoma koehleri*, maternal age or experience affected daughters' initial egg load and body size, whereas one tested maternal host-exposure treatment produced no detected effect [20]. The null result matters because it argues against treating every reproductive-history cue as consequential. In burying beetles, food deprivation delayed egg laying and reduced maternal care without reducing several measured offspring-performance outcomes [21]. Maturation stage can also change nutrient compromise rules even when absolute intake targets are not wholly distinct [22].

The proposed theory therefore separates immediate resource value from future reproductive opportunity. Immediate value concerns what acquisition supplies now—food, host access, or material for offspring—whereas future opportunity concerns what current action preserves, delays, or sacrifices in later reproductive contexts. The two may covary, but they need not. Nor is either a direct proxy for fitness. This distinction allows a reproductive state to increase the value of one resource while simultaneously making time, future competition, or remaining eggs more limiting.

*Predation and exposure costs*

Predation is a major exposure cost, but it is not a unitary behavioral variable. Field evidence shows that nonlethal predator presence can change visitation differently among herbivores, pollinators, and parasitoids, with responses also depending on predator hunting mode [23]. Enemy information can alter reproduction even when food acquisition is not measured: female *Drosophila* modify oviposition in response to parasitoid-associated information through sensory and octopaminergic processes [24]. A broader chemical-ecology synthesis likewise shows that food-, conspecific-, and predator-associated cues can guide female reproductive decisions in *Drosophila* [25]. These latter sources establish cue-sensitive reproductive decisions, not direct effects of parasitoids on food foraging.

Even within foraging contexts, behavioral direction cannot be collapsed into "risk aversion." Bumblebee anti-predator behavior varies with worker phenotype and context [4]. Ground beetles exposed to predation risk can become less choosy about food [9], indicating that risk can lower selectivity rather than simply terminate resource use. Field guild responses can also be weak, absent, or differently directed across predator modes [23]. Exposure cost should therefore describe what can be lost or encountered—injury, mortality, time, access, or reproductive opportunity—without prespecifying whether the behavioral response is avoidance, faster exploitation, reduced selectivity, persistence, or redirection.

The same logic extends beyond predators. In bed bugs, mating and starvation jointly alter host-seeking and feeding behavior [2], so host acquisition occurs within a state-dependent context rather than a simple hunger gradient. In provisioning solitary bees, interactions with males consume foraging time and can create a reproductive-interference cost distinct from predation [18]. The proposed theory therefore recognizes separate exposure classes rather than adding unlike hazards into one score. Predation, resource-associated danger, and sexual interference may all reduce the net value of a foraging action, but they operate through different mechanisms and may be detectable at different stages of a foraging bout.

A useful synthesis is to locate these costs along a proposed decision trajectory comprising cue evaluation, search or approach, resource exploitation, and post-acquisition reproductive opportunity. The trajectory is not a universal behavioral sequence or a quantitative time axis. It is a device for asking where a cost enters the decision and which state variables are relevant at that point. Direct foraging-risk evidence, reproductive-decision analogies, and social or phenotype modifiers must remain visually and inferentially separate.

Because prose cannot efficiently display how distinct exposure classes, evidence types, and boundary conditions map onto the same decision problem, **Table 1** organizes the cost states without converting them into a numerical risk scale.

**Table 1.** Exposure-cost states that change the interpretation of reproductive foraging decisions

| **Cost encountered** | | **Reproductive-state decision** | |
|---|---|---|---|
| **Exposure-cost domain** | **Foraging system and measurement** | **Risk–reward reweighting** | **Causal isolation** |
| **Predator-mediated resource exposure** | Ground beetles; bumblebee workers; mixed insect guilds. Food selectivity, approach/avoidance, or visitation changes in predator contexts | A higher exposure cost can change selectivity or resource use without requiring complete avoidance. Evidence-supported cost class; integration with reproductive state is proposed. | Direction varies with phenotype, guild, predator mode, and experimental setting. Manipulate reproductive state and predator context factorially while measuring both resource choice and exposure |
| **Enemy-information exposure** | Female Drosophila in parasitoid-threat contexts. Cue-dependent change in oviposition and associated sensory/neural processing | Threat information can alter reproductive decisions before any direct encounter. Evidence-supported reproductive-decision analogue. | Oviposition is not food foraging; laboratory transfer is limited. Test whether the same enemy information changes resource acquisition separately from oviposition |
| **Resource-associated acquisition hazard** | Female bed bugs seeking and taking blood meals. Host-seeking and feeding vary jointly with mating and energetic condition | Resource acquisition may become more valuable in one state while remaining costly to perform. Proposed exposure interpretation grounded in direct state-dependent feeding evidence. | Mating effects do not establish a general increase in risk tolerance. Separate resource motivation from direct measures of host-associated hazard |
| **Sexual-interference cost** | Provisioning solitary-bee females. Time spent rejecting or engaging males during flower visits | Reproductive interactions can reduce time available for offspring provisioning even when the resource remains valuable. Evidence-supported opportunity-cost class; placement in the common exposure taxonomy is proposed. | Published visit-loss consequence is a time-budget counterfactual, not measured fitness loss. Manipulate male encounter opportunity while measuring provisioning, mating, and later reproductive outcomes separately |
| **Phenotype- and context-conditioned exposure** | Bumblebee worker size classes; field insect guilds. Different responses to the same predator presentation or predator mode | Exposure cannot be assigned a fixed behavioral direction independently of phenotype and ecological context. Evidence-supported boundary condition. | Worker caste and community-level evidence are not individual female reproductive-state evidence. Stratify tests by phenotype, social role, taxon, and field versus laboratory context |

| | | | |
|---|---|---|---|
| **Cross-domain exposure boundary** | Foraging, mate choice, oviposition, and colony-resource studies. Similar state or cue sensitivity measured in different behavioral domains | Mechanistic or ecological analogies can generate hypotheses but cannot be treated as equivalent endpoints. Proposed inference rule. | Decision domains and levels of analysis are not interchangeable. Require direct measurement of the focal foraging behavior before claiming transfer |

**Figure 1** shows that for a different analytical purpose: rather than classifying exposure states, it shows where those costs can intersect a reproductive-state-dependent foraging trajectory while preserving the boundary between direct foraging evidence and proposed cross-domain integration.

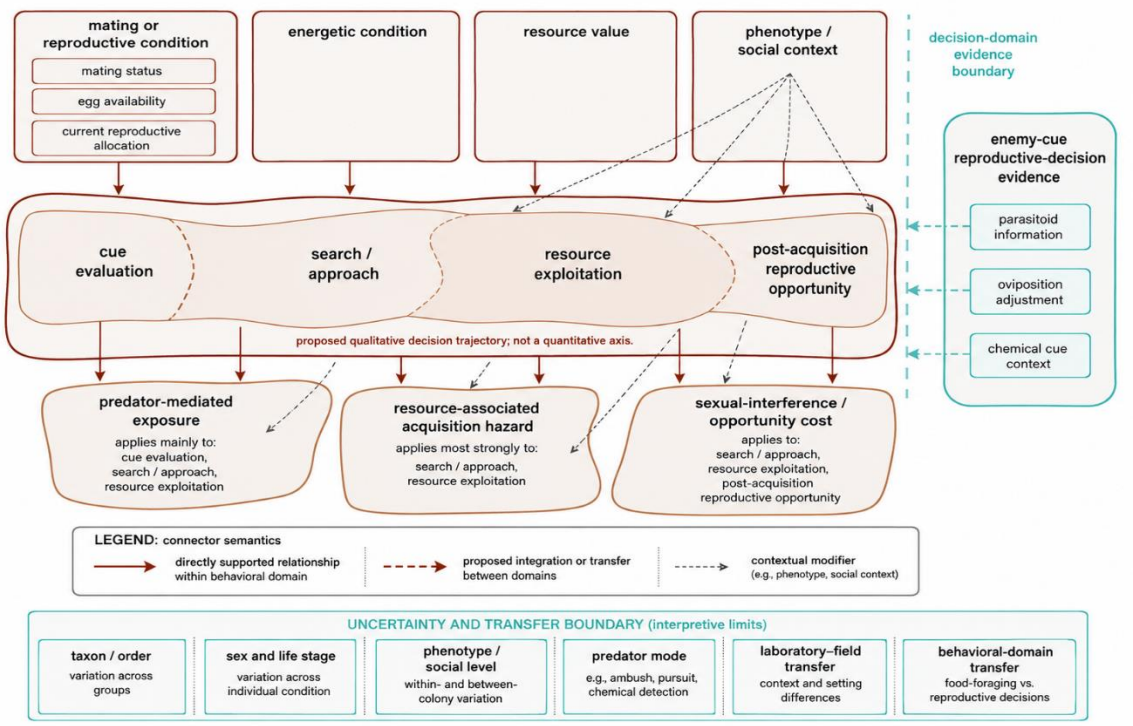



**Figure 1.** Reproductive-state trajectories traverse unequal exposure-cost fields

*Dynamic risk–reward surface*

The proposed dynamic risk–reward surface treats foraging as a qualitative decision landscape rather than a fitted optimum. Multidimensional trade-off surfaces already provide a defensible theoretical grammar for conditional life-history problems [7], but the present surface assigns no coefficients, thresholds, or universal axes. Its purpose is to represent how the relative value of a resource may change when reproductive condition, future reproductive opportunity, and exposure cost change together. A point on this surface should therefore be read as a conceptual decision region, not an estimated probability of foraging or a fitness maximum.

Reproductive state may shift the apparent reward gradient without altering the external resource itself. Internal state can change food-choice computations [1], mating can modify host-seeking and feeding in bed bugs [2], post-mating physiology can reweight nutrient choice [10], and reproductive neural remodeling can increase food intake [11]. These effects are biologically different, which is precisely why the surface does not collapse them into a single reproductive-intensity axis. The theory instead predicts movement between decision regions as the relevant state descriptor changes. Such movement need not represent a fixed increase in "risk tolerance."

Exposure remains an independent field. Phenotype can modify predator responses [4], predation can reduce food choosiness [9], and field responses vary among insect guilds and predator modes [23]. A reproductive-state effect can therefore occur while exposure sensitivity remains unchanged, and an exposure-driven behavioral change can occur without any reproductive-state mediation. This independence is important for experimental design because otherwise state-dependent motivation and risk-sensitive behavior become circular explanations of the same observation.

The surface is deliberately nonmonotonic. High resource quality can increase parasitoid activity despite egg depletion [3], while greater reproductive allocation can reduce later competitive ability [8]. Thus, the same

reproductive state can favor persistence at a valuable patch in one context yet favor restraint when future opportunity or exposure cost changes. **Figure 1** visualizes this distinction by separating evidence-supported state or cost effects from the article's proposed integration. Its topology should be tested against simpler alternatives, not assumed to describe every insect.

*Sex- and stage-specific predictions*

The framework yields conditional rather than universal sex differences. Female *Drosophila* studies show post-mating changes in feeding and sensory valuation [10], whereas male *Drosophila* can switch between feeding and courtship as hunger, food quality, and sexual opportunity change [16]. These findings justify sex-specific predictions but not a general claim that one sex is more risk prone. In other taxa, sex differences may instead reflect mating system, provisioning role, body size, dispersal behavior, or exposure ecology. A valid test must therefore specify which reproductive currency differs between sexes rather than treating sex itself as the mechanism.

Life stage and developmental history should be treated as independent modifiers of state-sensitive decisions. Nutritional state can reconfigure odor-guided behavior and early sensory processing in *Drosophila* larvae, while developmental thermal exposure can alter later bumblebee foraging behavior [26, 27]. Maturation stage also changes nutrient compromise rules in burying beetles [22]. Consequently, tests of reproductive-state effects should control developmental condition rather than attributing every age- or stage-associated behavioral difference to reproduction. The theory predicts the strongest interpretive errors where maturation, nutrient state, and reproduction change simultaneously but only one is measured.

Ovigeny generates a further prediction boundary. Egg load may influence parasitoid searching, but resource quality can override that relation [3]. Age and oviposition history also affect pro-ovigenic and synovigenic fig-wasp exploiters differently [19], and maternal history does not produce uniform effects on egg maturation [20]. The proposed prediction is therefore interactional: reproductive-state effects should depend on how eggs are matured, replenished, and converted into remaining opportunity, not on egg number alone. Comparable egg loads need not imply comparable future reproductive opportunity across contrasting ovigeny strategies.

**Results and Discussion**

The principal contribution of this theory is conceptual reconciliation. State-dependent food-choice mechanisms are established in particular systems [1], and multidimensional trade-off surfaces are established as theoretical devices [7], but the specific architecture developed here has not been empirically validated. Its novelty lies in separating reproductive state, immediate resource value, future reproductive opportunity, and exposure cost before asking how they interact. This separation converts an imprecise question—whether reproduction makes insects "riskier"—into a set of distinguishable hypotheses about valuation, cue processing, opportunity costs, and exposure.

That separation also explains why apparently contradictory responses need not be contradictory. Mating and starvation interact in bed-bug resource seeking [2]. Patch quality can override egg limitation in parasitoid activity [3]. Anti-predator responses vary with worker phenotype [4]. Food deprivation can alter maternal behavior without producing parallel declines in every measured offspring outcome [21]. A theory that predicts one directional effect of reproductive state would erase precisely the heterogeneity that the evidence requires it to explain. Null outcomes are likewise informative because they identify links that cannot be assumed merely from a change in state.

Transfer across taxa demands caution. Bumblebee colony state changes worker motivation [17], yet colony need is not individual reproductive state. Field predator effects differ among guilds [23], while chemical-cue evidence in *Drosophila* concerns reproductive decisions that may not transfer to food acquisition [25]. Developmental and larval-state evidence further shows that behavior can be reorganized by histories unrelated to adult reproduction. The framework should therefore be treated as hypothesis-generating across insects, with taxon, sex, stage, social organization, environment, and decision domain specified before prediction. Mechanistic generalization should be narrower still because much of the direct neural evidence comes from *Drosophila*.

Validation requires factorial designs that manipulate at least one clearly defined reproductive-state dimension, resource value or future opportunity, and an independently measured exposure cost. Behavioral endpoints should distinguish search, approach, exploitation, abandonment, and subsequent reproductive consequences rather than

compressing them into a single "risk-taking" measure. Laboratory tests can isolate mechanisms, but field tests are required to establish transfer under naturally varying predators, competitors, mating interference, and resource distributions. Competing simpler models—such as hunger alone, egg load alone, or fixed resource profitability—should be evaluated explicitly against the proposed state-dependent architecture. Repeated measures across reproductive transitions would be especially useful because they could distinguish stable individual differences from within-individual state effects without presuming either mechanism.

**Conclusion**

Reproductive state can change insect foraging decisions without imposing one universal direction of risk sensitivity. The proposed theory treats reproduction as a multidimensional decision variable that alters the balance among immediate resource value, future reproductive opportunity, and heterogeneous exposure costs. Its strongest prediction is conditionality: identical resources and hazards can produce different behavior when state, sex, stage, life-history strategy, or ecological context differs. The framework is therefore best regarded as a falsifiable organizing theory whose value depends on direct comparative and factorial validation.

**Acknowledgments:** None

**Conflict of Interest:** None

**Financial Support:** None

**Ethics Statement:** None

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